THE UNIVERSITY OF ALBERTA

# SENSE ORGANS OF THE MOSQUITO
# CULEX PIPIENS FATIGANS (WIEDEMANN)

by

© DOREEN ELAINE FROELICH

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS

FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

SPRING, 1971

Abstract

Culex pipiens fatigans (Wiedemann) has on its antennae five types of sensory receptors. These are two types of sensilla chaetica of varying lengths, two types of sensilla trichodea ($A_1$ and $A_2$), sensilla basiconica ($A_3$) and sensilla campaniformia. In the female about 1,200 thin-walled hairs and pegs are found on the 13 flagellar segments, but in the male, these are located only on the terminal two segments. In the female, type $A_1$ receptors remain fairly constant in number over the flagellum; type $A_2$ receptors decline in number from segments two to 13, while $A_3$ receptors increase over these segments. Culex pipiens pipiens (Linnaeus) and Culex pipiens molestus (Forskal) have the same receptor types and distribution pattern as Culex pipiens fatigans. The function ascribed to these receptors is discussed.

The labrum, labium, palps, halteres, wings, legs and ovipositor of Culex pipiens fatigans females were examined for sensory organs. Sensilla chaetica were found on all parts. The labella, tarsi and distal tips of the tibiae possess double-channeled hairs. The palps and labella bear sensilla basiconica. Sensilla campaniformia in groups are present on the halteres. The importance of these receptors in host finding, feeding, mating and oviposition is discussed.

Acknowledgements

I would like to thank my supervisors Dr. D. A. Craig and Dr. B. Hocking for their valuable assistance, criticism and patience in this work, and Dr. J. Sharplin for her help during the first stages of research. I am appreciative of the advice and assistance given by Dr. B. Heming. I am grateful to J.S. Scott, C. R. Froelich, A. Zalums, J. C. Shore and the late Dr. C. C. Steward and the graduate students in this Department for their kind aid.

I am indebted to the people who provided me with mosquitoes; Dr. A. W. A. Brown (University of Western Ontario, London, Ont.), Dr. A. Hudson (Entomology Research Institute, Ottawa, Ont.), Dr. A. Spielman (Tropical Public Health, Harvard University), and Dr. P. Belton (Canada Agriculture Research Institute, Belleville, Ont.)

Grateful acknowledgement is made of the financial assistance provided by the U. S. Army Grant No. 63 - G83 (Hocking Trust).

Autobiographical Sketch

After graduating from Grade XII (Senior Matriculation) in Medicine Hat, I entered the University of Alberta in Edmonton. Here I took a three year B. Sc. program in entomology, receiving the Entomological Society of Alberta Prize (1963). This formed my pre-medical requirement. I then spent one year in medicine at this University.

During the summer of 1964, I decided to enroll in entomology as a graduate student. I had become interested in neuroanatomy in medicine and wanted to work on some aspect of the nervous system of insects. Dr. J. Sharplin (Department of Entomology, University of Alberta) suggested I work on the sensory organs of a small insect and that I use the electron microscope. Dr. B. Hocking (Department of Entomology, University of Alberta) informed me that the U. S. Army was interested in the sensory organs of *Culex fatigans* because of the mosquito's importance as a vector for filariasis in tropical countries in which they had troops stationed.

List of Tables

List of Figures

Introduction

The purpose of this study was to examine the types and distribution of sensory receptors, primarily those on the antennae, of the mosquito, _Culex pipiens fatigans_. The distributions of sense organs on the antennae of the subspecies _Culex pipiens pipiens_ (Linnaeus) and _Culex pipiens molestus_ (Forskal) were also compared with that of _C.p. fatigans_ to see if differences in feeding behavior are reflected in sensory patterns. The types of sensory receptors found on the mouth-parts, legs, halteres and ovipositor of female _C.p. fatigans_ were studied. Behavioral work was attempted. The object was to ascertain the morphology and predict the function of the receptors present so that the behavior of the mosquito could be understood.

## 1. LITERATURE REVIEW

Many studies of sensory reception in insects have been done in the past. The earliest investigations attempted to locate the area of reception by observing the behaviour of the insect in the presence of an appropriate stimulus. The first experiments were aimed toward finding the site of olfaction. Lehmann (1799), comparing insects to vertebrates, concluded that this sense must be located in the stigmata or the tracheae. Later workers placed it on almost every part of the body. From 1838 to the present, an impressive amount of evidence suggests that the principal olfactory sites are on the antennae.

Forel (1908) gave a summary of the major works published to his time. Marshall's (1935) review of the olfactory location in insects covers the literature from the earliest works to 1935. His paper should be read for its critical review of the works of Fielde (1901-1932), Barrow (1907), McIndoo (1914-1933), von Frisch (1919-1930), Minnich (1929-1932) and others (Hartwell 1924, Glaser 1927, Valentine 1931, Marshall 1935). Several other reviews on chemoreception have been written by McIndoo (1914), von Frisch (1921, 1935), Dethier (1953, 1954), Hodgson (1955, 1958), Schneider (1964) and Slifer (1970).

In 1900, experimenters began amputating segments of the antennae to see if the insect still responded to odor. These methods were crude; there was little control of extraneous stimuli, and the results were often variable. It was not until the 1940's that an

olfactometer was used which minimized extraneous stimuli or kept them constant so that the effect of the stimulus under study could be determined. Attempts were also made to keep conditions constant during investigations of contact receptors. Even with these checks, the exact location of the receptors and the sensilla responsible for reception of the stimulus could not be found. Dostal (1958) worked on the distribution of chemoreceptors on the honey bee and the relationship between the number of receptors and the intensity of the reaction to odors. Ismail (1964) counted receptors on the antennae of female culicine and anopheline mosquitoes and studied their distribution patterns. Steward and Atwood (1963) made a similar study on Aedes aegypti (Linnaeus) and McIver (1969) examined Culex tarsalis (Coquillett) antennae. Aside from this, little has been done in determining the localization of sensilla on the antennae. The distribution of receptors on the palps, labella and the tarsi has received more attention. Because of the limited numbers of chemoreceptors on these organs and the presence of only one or two types of receptors, these studies have given excellent evidence as to the receptor responsible for contact chemoreception. The above factors also make these receptors ideal for electrophysiological study.

Dethier (1955), Hodgson (1955), Hodgson and Roeder (1954, 1956), Mellon and Evans (1961), Wolbarsht (1958), Wolbarsht and Dethier (1958), Tateda and Morita (1959), Morita and Takeda (1959)

and Morita (1959) investigated contact chemoreceptors on the blowfly electrophysiologically. A technique was developed using a fluid-filled micropipette placed over the tip of the receptor hair. The pipette electrode was used both as a recorder and as a source of chemical stimulation. Morita (1959) improved this technique by placing the pipette electrode through the hair wall and recording from there. An indifferent electrode was place in the head. Using these methods on the blowfly, Hodgson and Roeder (1956) discovered a neurone (designated L) which responded to salts and another (designated S) which responded to sugars. Wolbarsht and Dethier (1958) detected a third neurone (M) responsible for mechanoreception and Mellon and Evans (1961) recorded from a fourth neurone responding to water. Schneider (1957) has used these methods in investigating olfaction in Bombyx mori (Linnaeus). Electrophysiological techniques have thus opened a new field which has yielded the most conclusive evidence of receptor function.

With the use of such physiological methods, receptors can be identified as to function. In the past, however, function was often assigned to a structure because it conformed to a postulated standard form. The literature abounds with histological studies proposing conflicting functions for the same structure.

Sensory organs differ in cuticular and in cellular structure, each type having its own characteristic form. The cuticular part

may be in the shape of a hair, spine, scale, peg, pit, plate or pore. The cellular part varies in the number and arrangement of neurones, dendrites and associated cells. Snodgrass (1926) devised nomenclature for the various types. He also defined sensillum as "the receptor complex formed of the cuticula, the sense cells or group of sense cells, and the associated chitinogenous cells". His terminology is now accepted. Extensive light microscope studies since his time have elaborated on the histological structure. In this regard, the works of Slifer, Prestage and Beams (1959) and Hsu (1938) are most valuable.

The use of the electron microscope greatly extended the limits of resolution. Studies with it have revealed complexity in cellular and dendritic structure. Slifer and her co-workers have contributed immensely to our present knowledge. They did electron microscope studies of sensilla on the antennae of one or more representative species from each major order except Lepidoptera which was examined by Schneider and Kaissling (1957). In each species examined, thin-walled pegs with small pores on their surface were found. Fine filaments arising from the sides of the dendrites of the sensory neurones pass into these small openings in the peg wall and are exposed to the surrounding atmosphere. A ciliary structure in the dendrites, first reported in the tympanum by Pumphrey and Gray (1958), was also found. Adams, Holbert and Forgash (1965), Larsen (1962) and

Dethier and Wolbarsht (1956), examining contact chemoreceptors on the tarsi and labella with the aid of the electron microscope, found that the dendrite extended to the tip of the double-channeled hair through the thick-walled lumen. One distal fibre terminated at the base of the hair while the remaining ones terminated beneath the open pore in the papilla at the hair tip. In recent years, the electron microscope has received increased use in attempts to understand receptor function.

Familiar as mosquitoes are, studies of the structure and function of their sensory equipment received little attention until the 1950's. Johnston (1855) was the first to publish a description of the organ, later named after him, in a male mosquito antenna. Child (1894), Eggers (1924), Mayer (1874), and Risler (1953, 1955) further studied this auditory organ in the mosquito. Since then, Aedes aegypti has been the most thoroughly studied. Frings and Hamrum (1950) examined chemoreceptors on the tarsi and labella; Roth (1951), Roth and Willis (1952), Bar-Zeev (1960), Slifer and Brescia (1960), Slifer and Sekhon (1962) and Steward and Atwood (1963) studied the antennae. Owen (1963) and Feir, Lengy and Owen (1961) gave accounts of tarsal and labellar contact receptors in Culiseta inornata (Williston). Distribution and description of receptors of anophelini and culicini are found in papers by Ismail (1962, 1964). By far the majority of works, however, deal with attraction or repulsion of Aedes aegypti to a

variety of stimuli ranging from color to temperature to odors. No attempts were made in such experiments to determine the types of receptors present. Brown and others have attempted to find what makes the host attractive to mosquitoes. Other experiments have been carried out using repellents. Much more remains to be done in this field.

# 2. MATERIAL AND METHODS

## 2.1 Rearing

A colony of Culex pipiens fatigans (Wiedemann), Rangoon normal, was established with eggs, larvae and adults provided by Dr. A.W.A. Brown of the University of Western Ontario, London, Ontario. This species breeds continuously all year and is easy to maintain in the laboratory. The mosquitoes were kept in cages about 10" x 10" x 14". All larval and pupal stages were kept together in shallow trays filled with tap water changed every four to five months. The water level was maintained by adding water periodically. The larvae were fed a ground, 3:1 mixture of barley Pablum and yeast sprinkled on the water twice a week. The scum was removed from the trays several times a week. Adults were maintained on a 10% sugar solution and human blood.

Colonies of Culex pipiens pipiens (Linnaeus) and Culex pipiens molestus (Forskal) were kept for several months. C.p. pipiens were obtained from Dr. A. Hudson of the Entomology Research Institute, Ottawa, and C.p. molestus from Dr. A. Spielman, Department of Tropical Public Health, Harvard School of Public Health, Boston, Mass. C.p. pipiens were kept under conditions similar to C.p. fatigans except that they were allowed to feed on young chickens. C.p. molestus were kept in small lantern globes set on top of glasses filled with water. The adults were fed only on sugar. These mosquitoes

did not breed readily in the laboratory. Sufficient specimens were obtained, however, for counts of the receptors on the antennae.

2.2 Microscopy

The material used for examination under the light microscope was fixed in Bouin's, Carnoy's (with chloroform) or F. A. M. fixative. After fixation, dehydration and clearing, whole antennae of C. fatigans, C. pipiens and C. molestus were stained with acid fuchsin or methylene blue or left unstained. This material was mounted in balsam between two coverslips to enable counting of the receptors on all sides of the antennae.

The crystal violet technique developed by Slifer (1960) was used to locate permeable areas in the cuticle. Whole, fixed mosquitoes were placed between pieces of glass wool soaked in crystal violet.

Antennae to be sectioned were cut into pieces of three or four segments prior to embedding in order to allow the embedding material to penetrate into the lumen. The area of the paraffin block surrounding the specimen was melted with an electric needle and the specimen oriented in the plane required. Embedding in paraffin resulted in excessive shattering of the cuticle during sectioning. Good results were obtained using Peterfi's method of double embedding in celloidin and paraffin. Sections were cut at three, five or 10 microns.

Sectioned material was stained with Mallory's triple stain, Masson's trichrome method or Heidenhain's haematoxylin. For

staining nerves, Rowell's silver stain was used as well as Larsen's modification of Holme's silver technique (1960). The latter proved more reliable, although even with this method nervous tissue was only faintly stained.

Antennae to be examined with the electron microscope were cut into several pieces, fixed with buffered 2% osmium tetroxide and embedded in araldite (Palade 1952). They were sectioned on a Porter-Blum microtome using a glass knife. Sections of sufficient thinness were seldom obtained and those that were obtained proved worthless when viewed with the microscope.

A plexiglas box olfactometer was built for an intended study into the function of the antennal sensory receptors. A description of this olfactometer and its failure to work will follow in the section on behavioral work.

## 3. STRUCTURE OF THE ANTENNA

### 3.1 General

The bodies of mosquitoes have a generous covering of bristles and microtrichia. Sense organs are located on the proboscis, legs, halteres, ovipositor and the head. The antennae have a concentration of sense organs playing an important role in host finding, especially in the female (Roth 1951). The male antennae are modified for locating the female.

The antennae of the mosquito consist of a basal ring-like scape, a large globular pedicel and a flagellum composed of 13 articles which are sometimes referred to as segments or subsegments (Figs 1 and 2).

Three muscles arising on the anterior tentorial arms and inserted into the base of the scape, and other muscles running from the scape wall to the base of the pedicel move the antenna. No muscles extend into the flagellum. Two pivot-like processes on the head capsule and their corresponding articular points on the scape, permit movement in the transverse plane. Two similar articulations, almost at right angles to the others, between the scape and pedicel allow movement in the vertical plane.

Each antenna is innervated from a deutocerebral lobe of the brain (Snodgrass 1926). The antennal nerve runs through the scape and pedicel into the flagellum where it divides into two main trunks

which extend the length of the flagellum. Tracheae supply the antenna and a blood vessel from a pulsating organ located between the antennae runs through the centre of the scape, pedicel and flagellum, supplying their parts (Clements 1956).

3.2 Female Antenna (Fig. 1)

The antennal flagellum of the female Culex p. fatigans is about 2.23 mm long (average of five specimens). The first and 13th segments are the longest (0.20 mm and 0.22 mm respectively). The other 11 segments vary slightly in length from 0.16 to 0.17 mm. The diameter of the flagellum tapers gradually towards the tip, ending in two cones with a basal diameter of 5.2 microns. The first segment is 65 microns in diameter at its widest part with the flagellum narrowing to about 18 microns at the 13th segment. The band-like scape is 0.02 mm long and 0.18 mm wide. The pedicel is 0.09 mm long and 0.16 mm in diameter.

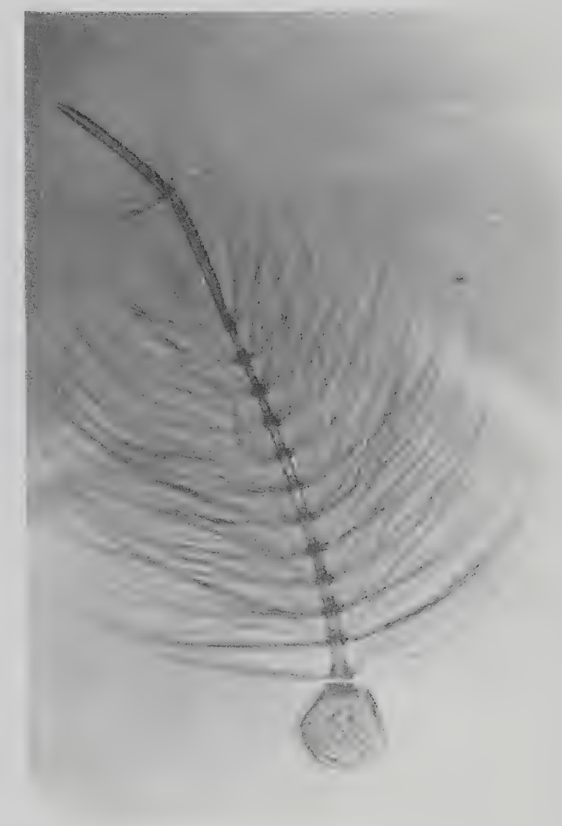
With the exception of the first and last flagellar segments, the 12 in between are similar. The proximal half of the first segment is more lightly pigmented than the distal half (Fig. 3). This lighter part is covered with microtrichia and lies partially within the concave distal end of the pedicel. The darker distal half bears approximately five scales and some microtrichia. This is the only segment of the flagellum which has scales and microtrichia. A few bristles of various lengths are found on the distal half. There is a ring of bristles at the

Fig. 1

0.5 mm

Whole mount of female _C. fatigans_ antenna, without the scape.

Fig. 2



0.5 mm

Whole mount of male _C. fatigans_ antenna, without the scape.

start of the pigmented area with a cluster of bristles just distal to these. Another ring of bristles occurs at the distal end of the segment. Several smaller bristles are scattered between the two rings. Thin-walled setae are found on the pigmented part, amongst the bristles.

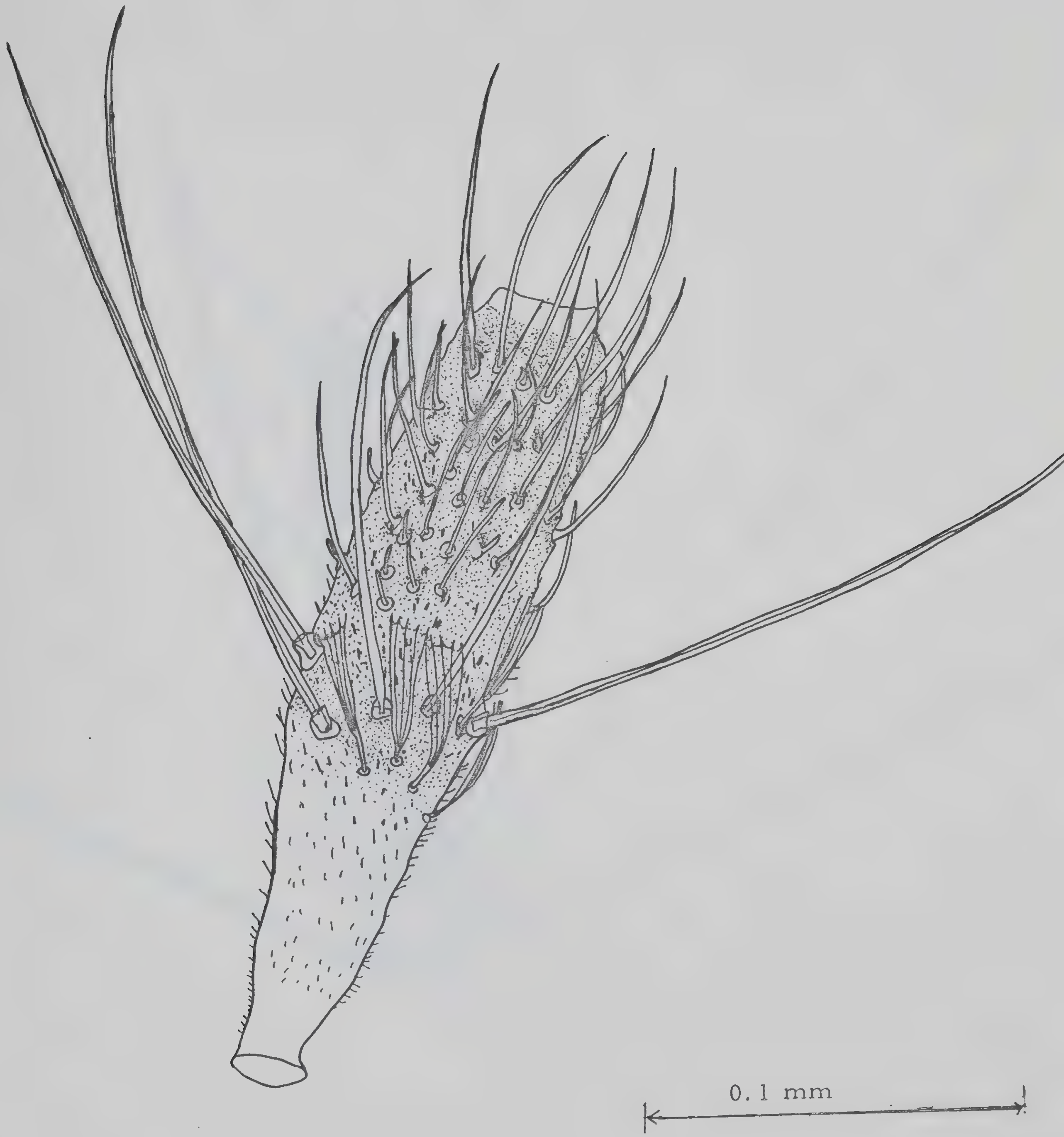
Segment 13, being the thinnest and longest, differs from the others because of the two small cones at the extreme tip (Fig. 5). One cone is slightly below the other. Each cone bears a campaniform sensillum at its tip. A ring of four medium sized bristles is found at the tip of the segment below the cones.

Segments two to 12 differ little from each other in size or structure (Fig. 4). These are pigmented except for a small proximal ring (about 1/6th the length of the segment) and a narrower distal ring. The junction between segments is pigmented. Each of these segments has a proximal whorl of six large bristles and one to several smaller bristles near the distal end. The major part of each of these and the 13th segment is covered by thin-walled sensilla of three types. These receptors are sensilla trichodea of two kinds - one sharp-tipped and the other blunt-tipped - and sensilla basiconica, small and thorn-shaped. There are also one or two campaniform sensilla present on some segments.

The scape is a narrow, irregular band with two notches which articulate with the head capsule. It has microtrichia.

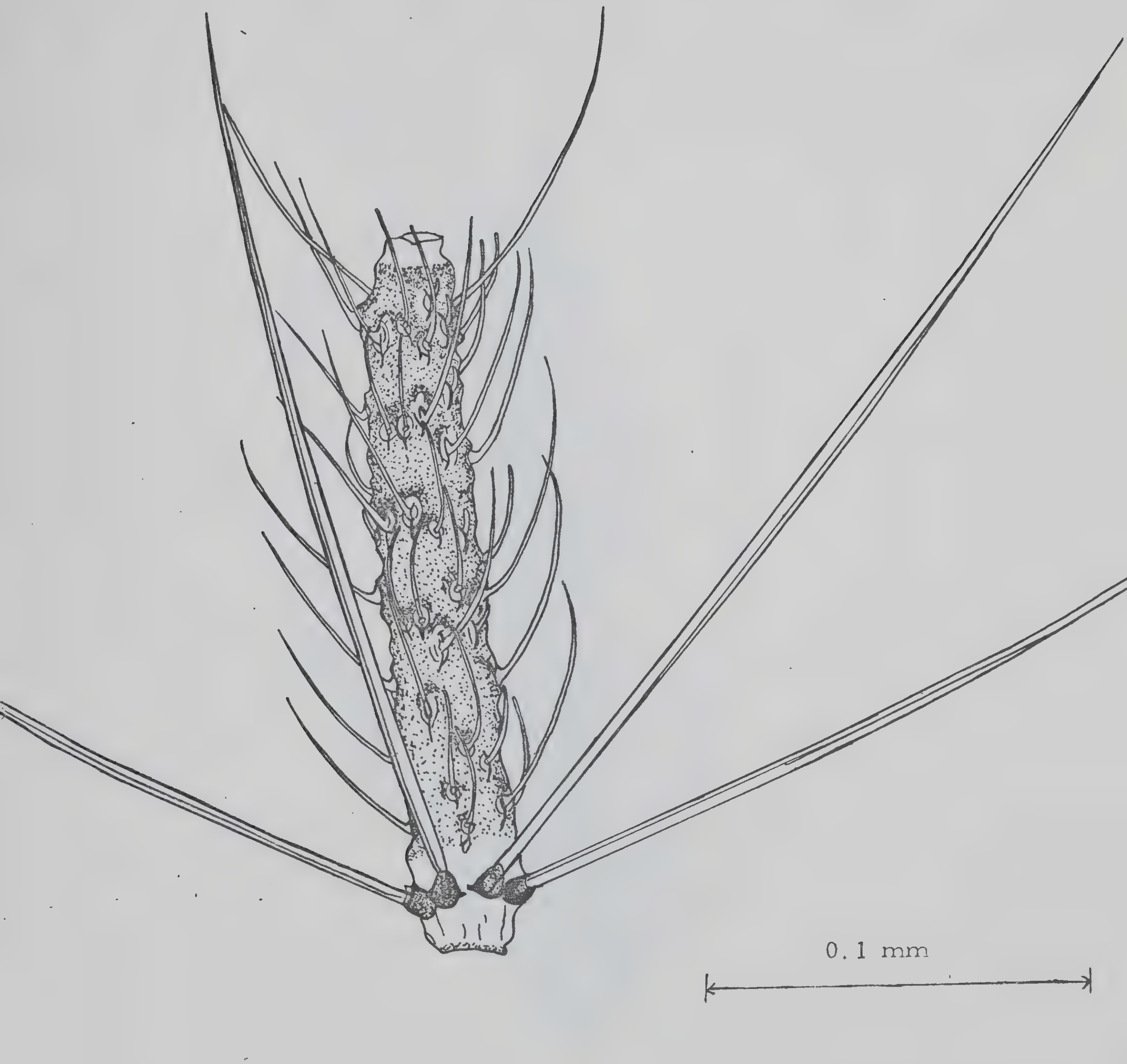
Fig. 3






1st flagellar segment of female C.p. fatigans antenna

Fig. 4




7th flagellar segment of female C. p. fatigans antenna

Fig. 5


13th flagellar segment of female C.p. fatigans antenna

The pedicel of the female is globular with a deep invagination at the distal end into which part of the first flagellar segment fits. Besides a covering of microtrichia, the pedicel has five bristles and two or three scales. Most of the interior is taken up by the elaborate scolopophorous Johnston's organ. Although not as large in the female as in the male, its structure is similar in both. A description will follow in the section dealing with the male antenna.

### 3.3 Male Antenna (Fig. 2)

The antennal flagellum of the Culex p. fatigans male is shorter and wider than that of the female, being about 1.81 mm long (an average of five specimens) and consists of 13 segments. The first, 12th and 13th segments are the longest (0.17 mm, 0.41 mm and 0.38 mm respectively). The second (0.07 mm) to 11th (0.09mm) segments increase in length gradually. The width of the first segment is about 55.5 microns with the following 10 segments decreasing in width. The 11th segment has a diameter of 15 microns. The diameter of the 12th is 22.6 microns and the 13th is 23.5 microns. The male scape is 0.03 mm long and 0.24 mm wide. The pedicel (0.10 mm long and 0.23 mm wide) is larger than that of the female.

The proximal 11 flagellar segments are all similar in appearance. They are very different from the corresponding segments in the female. Each possesses an unpigmented proximal portion which has no receptors

of any kind. Distal to this is the pigmented, saddle-shaped, wider part (about 2/5th the total segment length) bearing a conspicuous whorl of long bristles on its proximal margin. The whorl is not complete; there is a gap in it on the ventral side. There are between 29 and 39 long bristles in each whorl. In the mature male, the bristles stand out at nearly right-angles to the long axis of the antenna while in the newly emerged male they lie against the antennal shaft. Roth (1948) described these bristles as capable of detecting sound vibrations. The remainder of the pigmented part is covered with microtrichia. The first flagellar segment has, in addition to the whorl, several smaller bristles similar to those found on the first flagellar segment of the female, about six scales, and is covered by microtrichia. None of these 11 segments bears thin-walled hairs.

Segment 12 is transitional between the last and remaining proximal segments. Its base is unpigmented and the whorl of bristles occurs near this end. From here microtrichia extend about half way up. The distal half bears thin-walled hairs and small bristles. Thin-walled hairs with pointed ends are most numerous on the 13th segment, as are the thorn-shaped receptors, while slightly more blunt-tipped hairs occur on the 12th than on the 13th segment.

The first to 11th segments of the male antennal flagellum possess an outer and an inner skeleton. The ectoskeleton bulges outward from the intersegmental membrane and attaches onto the saddle. The

endoskeleton forms a cylinder running from base to apex of each segment. The two antennal nerves, the blood vessels, the trachea and the epidermal and nerve cells lie within the inner cylinder. The endoskeleton is perforated by two oval openings opposite one another. The endoskeleton strengthens the male antenna and is completely formed 24 to 30 hours after emergence from the pupal case (Steward 1959). In old males, it may be all that is seen. The ectoskeleton becomes shrunken and wrinkled. Expansion of the long bristles in the whorls occurs at the same time that the endoskeleton is formed.

The scape in the male is similar to that of the female but is larger in size.

The pedicel of the male mosquito has undergone extensive study because of the enlarged Johnston's organ it possesses and the role it plays in detecting movement of the antennal shaft set up by vibrations detected by the bristle whorls (Roth 1948).

In sections of both male and female C.p. fatigans antennae the outer surface of the pedicel is seen to be deeply invaginated forming a depression or pit (Fig. 6). The cuticle at the basal part of the pit is a thin membrane (MBR) reinforced by rib-like cuticular thickenings (CR). The articular membrane and ribs are attached at the base of the pit to a circular basal plate (PL). An opening in the centre of the plate allows the base of the flagellum to fit into it. Radiating from the plate is a series of 60 cuticular rods (R) which curve upwards within the

pedicel. From the bottom of these rods project small chitinous processes (CP) to which the terminal filaments (F) of the radial scolopophora are attached. The terminal filaments are surrounded by the two cap or envelope cells ($C_1$ and $C_2$) lying in two rows. The sensory cells (SC) are arranged in a ring two or more thick outside of the cap cells. The cap cells and sensory cells with their filaments occupy almost the entire pedicel. Anterior scolopophorous organs (ASO) comprise a ring situated between the rods and the articular membrane. The posterior series of scolopophora (PSO) lies below the basal plate, extending along the longitudinal axis of the antenna, with their terminal filaments running into the epidermal cells lining the plate. The axons from the sensory cells join the antennal nerve which has an opening to permit blood vessels and trachea to pass through. My description is much like that given by Risler (1955) and Steward (1959) for *Aedes aegypti*.

Fig. 6

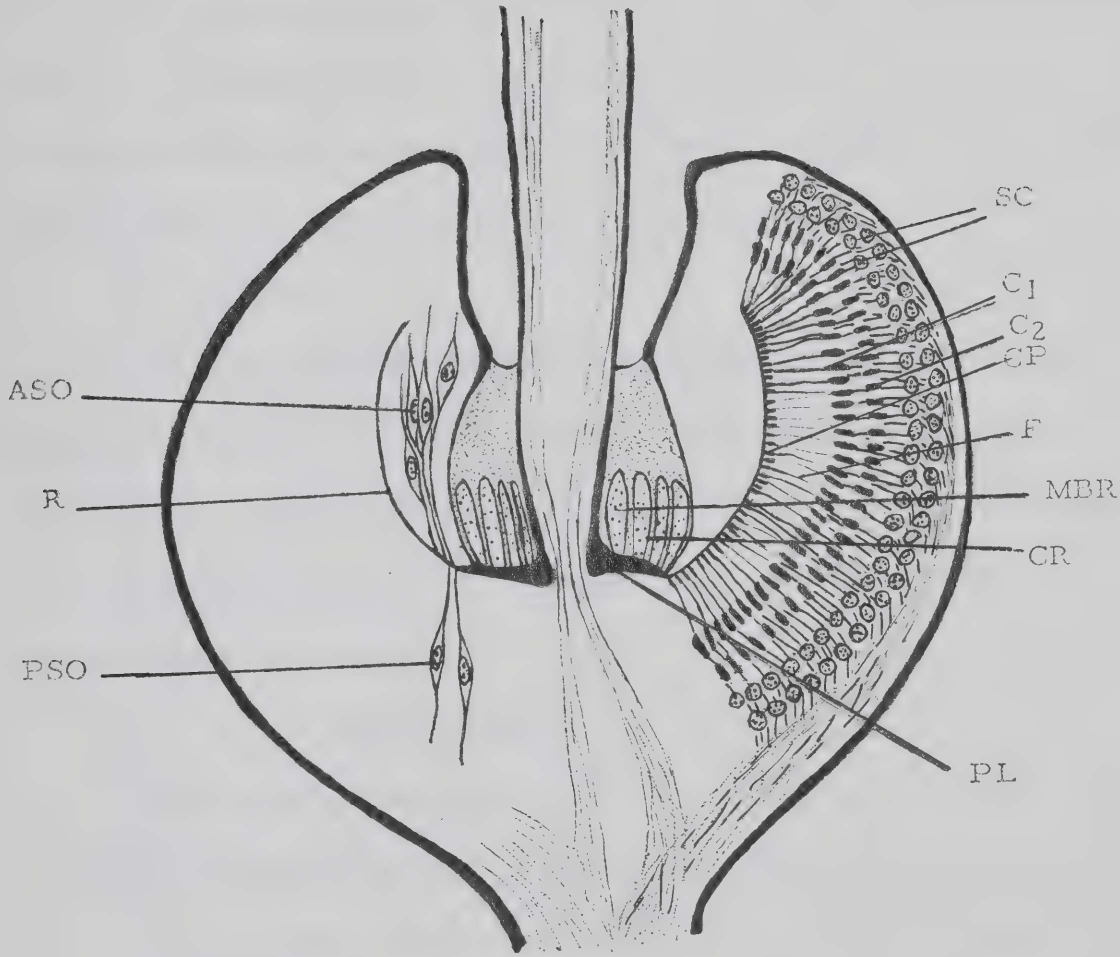



Diagram of Johnston's organ in the pedicel of the antenna of male <u>C. p. fatigans</u>. The posterior and anterior series of scolopophora are omitted from the right side while the radial series is omitted from the left side of the drawing.

| | | | |
|---|---|---|---|
| ASO | - anterior series of scolopophora | | |
| PSO | - posterior series of scolopophora | | |
| R | - cuticular rods | F | - terminal filaments |
| SC | - sensory cells | MBR | - articular membrane |
| $C_1$ | - cap cell | CR | - cuticular ribs |
| $C_2$ | - cap cell | PL | - basal plate |
| CP | - chitinous processes | | |

# 4. SENSORY RECEPTORS ON THE ANTENNAL FLAGELLUM

Five kinds of sensory structures can be found on the antennal flagella of Culex pipiens fatigans females and males. While male and female antennae have the same sensory receptors, the female antenna is better supplied with the thin-walled receptors. The detailed examination was restricted to the female flagellum.

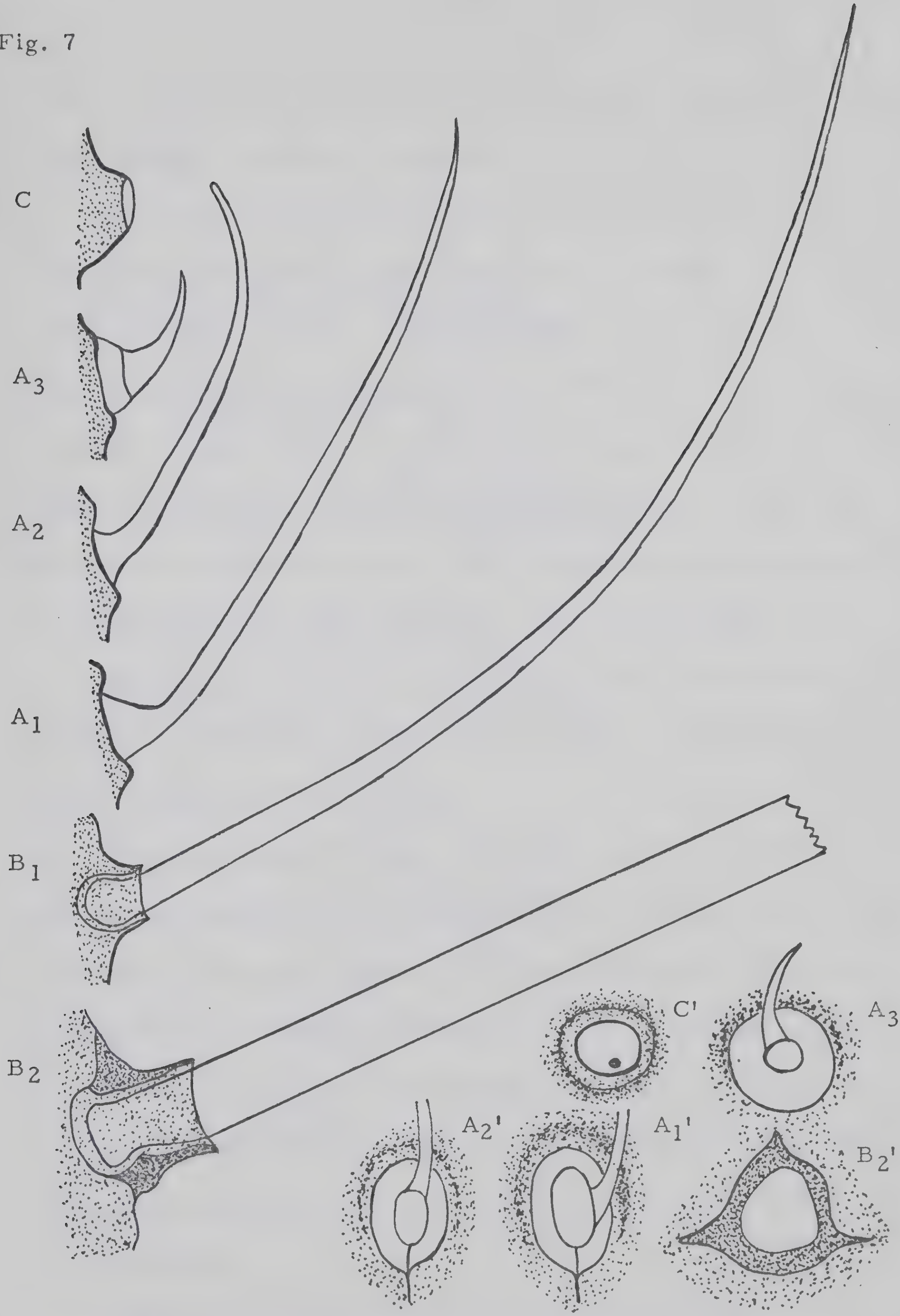
## 4.1 Bristles

There are two types of thick-walled bristles whose only conspicuous difference is in their average length and their position on the antenna. One type is longer and is arranged in whorls, the other is smaller and is found at the segments' tips and on the distal half of the first flagellar segment.

### 4.1.1 Large Bristles

The bristles arranged in whorls are larger and more numerous in the male than in the female. In the female, these bristles arise near the base of segments two to 13 in whorls of six. The first flagellar segment has four to six large bristles but these are not in a whorl. Large bristles are the largest hairs on the antenna. In the female, their average length decreases from 450 microns on segment two to 169 microns on segment 13. The length of those on segment one ranges from 141 to 231 microns. Four such bristles, 132 to 164 microns long, are found just below the cones of segment 13. (These lengths are the average of all those found on five flagella). McIver (1969)

Fig. 7




Six types of sensory receptors found on the antennal flagellum of <u>Culex fatigans</u>. C, $A_1$, $A_2$, $A_3$, B1 and B2 are in lateral view. C' to B2' are bases of receptors in top view.

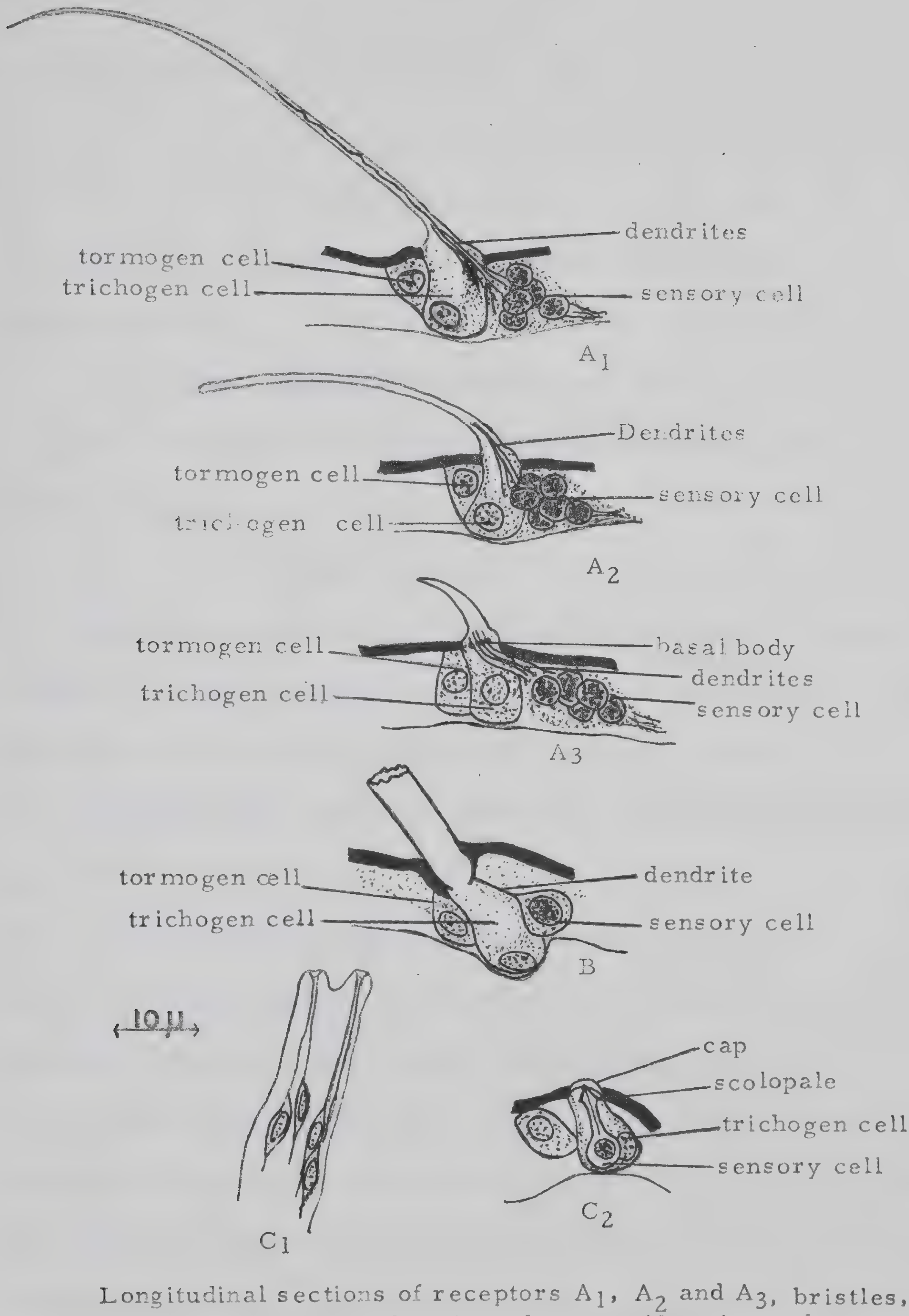
found a similar distal decrease in length of large bristles on female Culex tarsalis (Coquillett) antennae.

The large bristles (Fig. 7, $B_2$) are rigid, dark-colored, curved throughout their length and the tips are pointed. A lumen can be seen running to the tip. The base of the bristle is set into a cup-shaped socket which is strengthened by a distal keel and two lateral ones (Fig. 7, $B_2'$). The sockets are darkly sclerotized and raised keels are readily visible under the microscope. The females, in which the bristles are fewer and therefore less crowded, have larger keels than the males where the lateral keels are often missing entirely.

Under an oil immersion lens (mag. x 1200), longitudinal ribs on the bristle surface can sometimes be seen coiling its entire length. Slifer and Sekhon (1962) sectioned these bristles and examined them with the electron microscope. They found that in cross-section the bristle is somewhat star-shaped with five, six or seven points present. The points of the stars represent the lines visible under the light microscope. The entire surface of the bristle is scalloped, the grooves of these scallops running parallel to the long lines. Slifer concluded that perhaps the rough surface of the bristle increases the response to sound waves by creating greater friction between it and the atmosphere.

Sections of the base of the bristle show a large vacuole beneath the bristle (Fig. 8, B). A single neurone is associated with each bristle. Occasionally a dendrite was found running from

Fig. 8




Longitudinal sections of receptors $A_1$, $A_2$ and $A_3$, bristles, the terminal campaniformia and campaniformia on the first segment, of female C. p. fatigans antennae.

the neurone to the base of the bristle. The exact attachment of the dendrite to the bristle base was never visible but the dendrite ended near the base since it was never seen in the bristle lumen. A trichogen cell was present, its large vacuole extending into the base of the bristle.

Long, intact, undamaged bristles never stained when placed in a solution of crystal violet, a stain useful for detecting permeable sense organs.

#### 4.1.2 Smaller Bristles

Smaller, pointed bristles located on the distal half of segment one and at the tips of segments one to 12 decrease gradually in length from 89 microns on segment one to 52 microns on segment 12.

Examined under the microscope, they closely resemble the larger bristles (Fig. 7, $B_1$). The sockets are basically the same as those described for the larger bristles, except that the keels are smaller. A single neurone is located at the base of each bristle adjacent to the large vacuole of the trichogen cell, just as in the larger bristles (Fig. 8, B). None stained with crystal violet dye when intact and unbroken. The only major difference between the two types of bristles is in their length and location. Yet even in length there is a considerable range. In the larger bristles, the greatest length measured was 470 microns and the smallest 132 microns. In the smaller bristles, the longest was 127 microns and the shortest 52 microns.

4.2 Thin-Walled Hairs

The antennal flagellum of C. fatigans has three types of thin-walled hairs which will be called $A_1$, $A_2$ and $A_3$ after similar hairs found by Steward and Atwood (1963) on the antennae of Aedes aegypti.

4.2.1 Sharp-tipped Hairs

Sharp-tipped $A_1$ hairs vary in length from 55 to 70 microns on a single antenna. They are almost colorless and transparent and can easily be distinguished from the bristles. $A_1$ hairs taper towards their tips (Fig. 7, $A_1$). They curve sharply near their base and slightly near their tip toward the flagellar shaft. Sockets similar to the ones on the bristles are not present. The base of the hair is surrounded by a thin, oval membrane encircled by a thin rim of darker cuticle (Fig. 7, $A_1'$). A thin, raised strut extends from the hair base to a spur off the darker rim. This strut apparently serves to support the hair. The lumen of the hair extends to the tip but is very narrow near the end.

Four or five neurones innervate each hair (Fig. 8, $A_1$). These are located beneath the hair base, usually proximal to the base. A large trichogen cell with a vacuole extending into the hair base lies directly under the hair.

When the antenna was stained with a solution of crystal violet, applied externally, the tips of undamaged $A_1$ receptors were stained. In some cases, about one-third of the distal part was stained. After

being mounted for 24 hours in balsam, the stain still remained at the tips of $A_1$ hairs while other receptors previously stained became colorless. Slifer and Sekhon (1962) did not get these receptors to stain when they used this technique on A. aegypti antennae.

4.2.2 Blunt-tipped Hairs

Blunt-tipped $A_2$ hairs are of two types - one being longer and sharper (type I) and the other being shorter and blunter (type II). $A_2$ type I hairs vary in length on a single flagellum from 25 to 37 microns. Characterized by their thin walls and rounded tips, the hairs curve sharply at their base to parallel the flagellar shaft (Fig. 7, $A_2$). They do not diverge from the shaft as far as $A_1$ hairs. $A_2$ hairs taper toward their tips. The hair is surrounded by an oval membrane with a rim and strut like that described for $A_1$ sensilla (Fig. 7, $A_2'$). However, the base of the hair is narrower and the membrane smaller than that of $A_1$ receptors giving the base of $A_2$ sensilla a more delicate appearance. The lumen extends to the tip of the hair and under oil immersion (mag. x 1200) the cuticle at the tip looks thinner than the rest.

Six neurones were visible for each sensillum when sections of antennae were examined under the light microscope (Fig. 8, $A_2$). Also present were the two formative cells, the trichogen and the tormogen. The cellular arrangement of $A_2$ hairs is very similar to that of $A_1$ hairs except for more sensory cells and a smaller vacuole beneath the hair base. In a few slides the dendrites were observed to go part way up the hair lumen. No connection between the dendrites

and hair wall was seen. Slifer and Sekhon (1962) found that similar hairs in A. aegypti examined under the oil immersion lens showed the hair surface to scintillate as the focus was changed. Electron micrographs obtained by them revealed the wall of the hair to be perforated by numerous holes with an external diameter of 0.05 microns. Branches from the sides of the dendrites were seen. In the grasshopper, Melanoplus differentialis (Thomas) similar dendritic branches were shown by these authors to extend into the pores of the hair wall, but they were unsuccessful in getting similar preparations from A. aegypti.

When crystal violet stain was applied to the intact flagellum, $A_2$ hairs stained over their entire length. Of the two hair types stained, $A_2$ stained more intensely. After being mounted 24 hours in balsam almost all $A_2$ hairs initially stained were colorless.

Type II $A_2$ hairs were first reported by Ismail in 1964. Type II hairs have a very blunt tip and are shorter and lie closer to the flagellar shaft than type I. They are from 16 to 21 microns long. Unlike the other thin-walled sensilla on the flagellum, these hairs do not taper. In all other aspects, they are indistinguishable from $A_2$ type I hairs. Sections through this type of hair were not obtained because of their limited number on the antennal flagellum.

Type II $A_2$ hairs stained the same as type I hairs when the antenna was placed in crystal violet stain.

### 4.2.3 Thorn-shaped Pegs

Thorn-shaped sensilla basiconica ($A_3$) are pointed-tipped pegs

nine to10 microns in length (Fig. 7, $A_3$). They surve slightly and project out from the flagellar shaft. The pegs have large bases set on a small prominence. Unlike the other two hairs, the round, clear membrane at the hair base has no sclerotized strut (Fig. 7, A3'). Under the microscope, the membrane appears dome-shaped and almost colorless. A clear area can be seen at the peg tip and a clear band just distal to the base is visible. The cuticle of the peg wall seems to be thinner here. The broad lumen at the base narrows near the tip but according to electron micrographs obtained by McIver (1969) it extends to the peg tip.

Viewing sections of the antenna under an oil immersion lens (mag. x 1200) disclosed the presence of at least five sensory cells associated with each peg (Fig. 8, $A_3$). These neurones often are found a short distance from the peg base towards the basal part of the segment, in a group under the flagellar epidermis (Fig. 8, $A_3$). A tormogen cell and a trichogen cell with its large vacuole reaching into the peg base lie directly beneath the peg. In longitudinal section, several darkly stained spots could be seen on the dendrites just before they entered the peg lumen. Prior to 1961 these dark spots were called Riechstabchen or olfactory rods but since then Slifer and Sekhon (1961) have shown them to be the basal bodies of cilia strengthening the dendrites. In my sections, the dendrites could not be seen beyond the point where they entered the peg lumen.

A3 pegs did not take up any crystal violet when they were placed in the stain. Of the three types of thin-walled hairs on the antenna, they were the only ones not to stain with crystal violet.

4.3 Sensilla Campaniformia

Sensilla campaniformia occur on a few segments of the antennae of female C. fatigans Those present on segment one, 10 and 12 are alike in structure. The two found on the cones at the tip of segment 13 differ somewhat from these in structure. Sensilla campaniformia are about three microns in diameter and two microns in length. In top view, these sensilla have a dark, circular rim (Fig. 7, C'). The cap-shaped dome is light in color with a dark circular dot visible under it. By focusing up and down, a line-like structure can be seen running inwards from this spot. In side view, the dark cuticle extends outward from the flagellar wall and a light colored, small cap covers the end of it (Fig. 7, C). The two sensilla at the tip of the 13th segment are set inside the pits at the tip of the cones (Fig. 8, $C_1$). One cone is slightly longer than the other. McIver (1969) stated that the opening in one cone is not the same as that of the other with one being larger and the structure within more prominent.

Several sections were made through a campaniform receptor located on the first flagellar segment. A single sense cell is present (Fig. 8, $C_2$). The cell body is large and spherical with a very darkly stained, eccentrically placed nucleolus in the nucleus. No axon was present in these sections. The distal process of the cell is elongated

and the end of it widened into a barb-like structure which appeared cuticular. This structure may be the scolopale. It ends in a point where it meets the cuticle of the external dome of the receptor. A filament is visible in the dendrite extending to the point of the barb. The scolopale probably is the dark spot visible from the exterior and the line running from it is the filament within the dendrite. A trichogen cell is seen surrounding the sensory cell.

The sensilla campaniformia located in the terminal cones of segment 13 are distinctive in that the dome of the receptor is set within a shallow pit at the cone's tip (Fig. 8, $C_1$). The dome does not appear to be of thicker cuticle than the cone wall. Two processes, each arising from a single sensory cell, extend to the sides of the dome. These processes are darker in their distal half where they are very narrow. Proximally, they widen as they become part of the sense cell body which is large and elongated with a large oval nucleus. The sensory cells always stained very faintly in methylene blue, acid fuchsin, and silver stains so that the processes could not be seen within them. The sensory cells are located at about the level of the terminal bristles. No other associated cells were seen near them.

## 5. DISTRIBUTION OF SENSORY RECEPTORS ON THE ANTENNAE OF C.P. FATIGANS, C.P. PIPIENS AND C.P. MOLESTUS FEMALES

The polytypic Culex pipiens species has puzzled taxonomists for years. Within the Culex pipiens complex are genetically distinct autogenous (laying eggs without a blood meal) and anautogenous biotypes. Culex fatigans is a tropical form frequently feeding upon man and other animals in nature. It is morphologically distinct from the pipiens and molestus forms and appears less host specific. Blood meals are required the year around. The pipiens form of the temperate zone generally feeds upon birds in nature. It is the most fecund. Because of the cold climate and obligate blood feeding habit, it hibernates. The molestus form is also temperate but does not need a blood meal to lay eggs. This allows it to live in sheltered, confined locations where host animals would not be found. A second egg clutch is deposited only after a meal of blood. In nature, these three forms are usually isolated geographically, reproductively or ecologically, but in the laboratory and in regions of overlap, hybrids occur. Because of the contradictions of relationship within the complex, it is difficult to affix a taxonomic status to these forms. However, in this study they will be dealt with as subspecies. A review of this problem is presented by Spielman (1964).

The distinct difference in feeding habits within the species led to this comparative study of distribution patterns of sensory receptors on the antennae of the above three subspecies.

The distribution of the bristles, the thin-walled trichodea and basiconica and the campaniformia sensilla on the flagellar segments of

the antennae of female C.p. fatigans, C.p. pipiens and C.p. molestus is shown in Table I. (All numbers are an average of 10 antennae examined for C. fatigans and five for C. pipiens and C. molestus). The basal segment has a cluster of bristles of various lengths scattered around the middle. The number of these is variable (from 13 to 22 per segment in the antennae examined). Distal to this group is a ring of bristles at the tip of the segment resembling the short bristles found on other segments. The number of these is between eight and 13. Because of the variations in length and number, the bristles on the basal segment are listed as undifferentiated in Table I.

The remaining 12 segments each bear six long bristles on their basal part in each subspecies, with the total number, excluding those on the first segment, being 72 plus three or four of these bristles located proximal to the apex of the last segment. Shorter bristles located near the tip of each segment except the last have the maximum number on the basal segments and decrease toward the tip of the antennae. C. pipiens has a few more of these bristles on the entire flagellum than the other two subspecies.

The three types of thin-walled sensilla covering the flagellum are pointed-tipped ($A_1$) and blunt-tipped ($A_2$) sensilla trichodea, and sensilla basiconica (A3). The number of $A_1$ sensilla differs little. C. fatigans has 464, C. pipiens has 468 and C. molestus has 425 $A_1$ hairs. However, C. fatigans with 485 and C. pipiens with 492 $A_2$ hairs differ from C. molestus with only 389 $A_2$ hairs. The distribution pattern is also different. In C. fatigans, type $A_1$ sensilla increase from 15 on the first segment to 40 on the second (Fig. 10). The number fluctuates between 33 and 39

TABLE I

Distribution and number of sensilla on the flagellar segments of the antennae of female mosquitoes

| | Thick-walled | | | | | | Thin-walled | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Sensilla Trichodea | | | | | | Sensilla Basiconica | | | Sensilla Campaniformia | | |
| | Long Bristles | | | Short Bristles | | | Pointed-tipped $A_1$ | | | Blunt-tipped $A_2$ | | | $A_3$ | | | C | | |
| Flagellar Segment | C. fatigans | C. pipiens | C. molestus | C. fatigans | C. pipiens | C. molestus | C. fatigans | C. pipiens | C. molestus | C. fatigans | C. pipiens | C. molestus | C. fatigans | C. pipiens | C. molestus | C. fatigans | C. pipiens | C. molestus |
| 1 | Undifferentiated | | | | | | 15 | 12 | 6 | 37 | 35 | 19 | 12 | 16 | 16 | 2 | 1 | 1 |
| 2 | 6 | 6 | 6 | 8 | 8 | 6 | 40 | 40 | 33 | 68 | 63 | 42 | 16 | 22 | 20 | 0 | 0 | 0 |
| 3 | 6 | 6 | 6 | 6 | 7 | 6 | 39 | 42 | 38 | 61 | 62 | 43 | 15 | 22 | 17 | 0 | 0 | 0 |
| 4 | 6 | 6 | 6 | 4 | 4 | 5 | 38 | 39 | 34 | 50 | 56 | 44 | 14 | 20 | 17 | 0 | 0 | 0 |
| 5 | 6 | 6 | 6 | 2 | 3 | 3 | 38 | 40 | 39 | 47 | 48 | 40 | 15 | 20 | 17 | 0 | 0 | 0 |
| 6 | 6 | 6 | 6 | 1 | 3 | 2 | 34 | 38 | 38 | 44 | 44 | 40 | 14 | 19 | 16 | 0 | 0 | 0 |
| 7 | 6 | 6 | 6 | 1 | 2 | 1 | 35 | 37 | 36 | 40 | 40 | 36 | 16 | 19 | 17 | 0 | 0 | 0 |
| 8 | 6 | 6 | 6 | 1 | 2 | 2 | 36 | 37 | 33 | 35 | 34 | 28 | 15 | 18 | 16 | 0 | 0 | 0 |
| 9 | 6 | 6 | 6 | 1 | 1 | 1 | 33 | 38 | 31 | 28 | 26 | 21 | 18 | 20 | 19 | 0 | 0 | 0 |
| 10 | 6 | 6 | 6 | 1 | 1 | 1 | 36 | 36 | 36 | 20 | 22 | 21 | 19 | 21 | 20 | 1 | 1 | 1 |
| 11 | 6 | 6 | 6 | 1 | 1 | 1 | 33 | 34 | 35 | 20 | 21 | 22 | 20 | 21 | 19 | 0 | 0 | 0 |
| 12 | 6 | 6 | 6 | 1 | 1 | 1 | 35 | 33 | 35 | 19 | 20 | 17 | 23 | 24 | 20 | 1 | 1 | 1 |
| 13 | 6+4 | 6+3 | 6+3 | 0 | 0 | 0 | 52 | 42 | 31 | 16 | 21 | 16 | 26 | 25 | 23 | 2 | 2 | 2 |
| Total | 76 | 75 | 75 | 27 | 33 | 29 | 464 | 468 | 425 | 485 | 492 | 389 | 223 | 268 | 237 | 6 | 5 | 5 |

Values for C. p. fatigans are the average of 10 antennae whereas those of the other two subspecies are the average of 5 antennae.

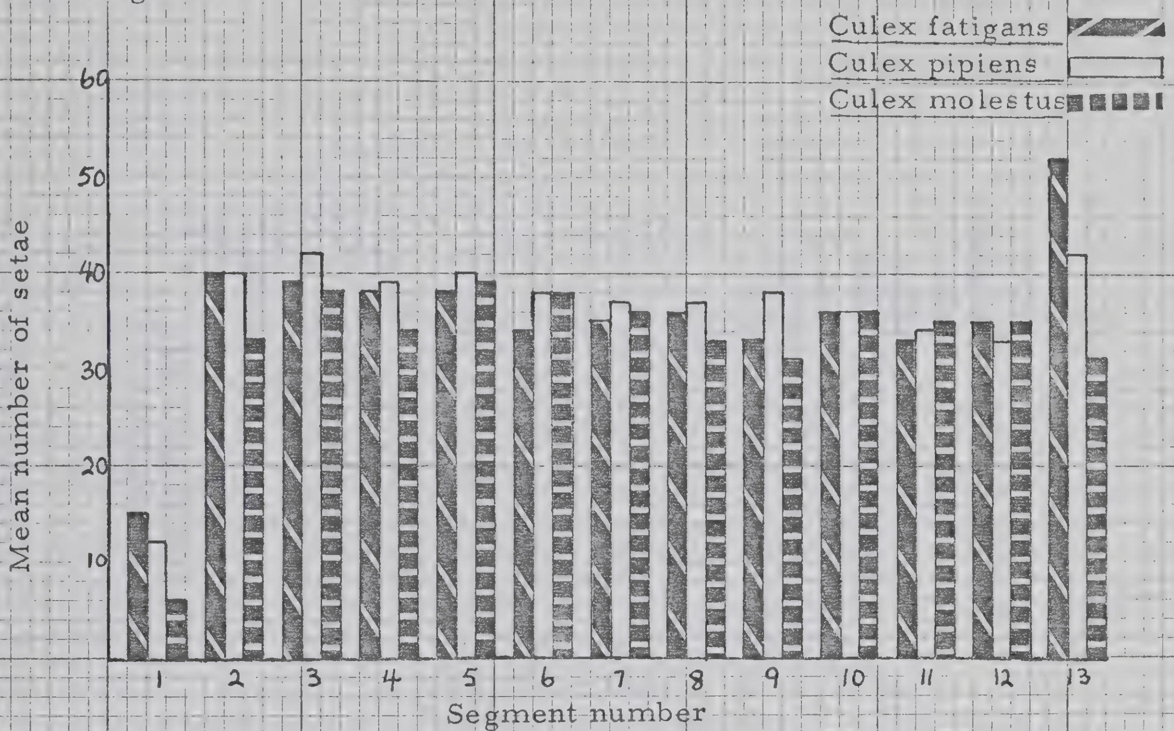
on the following segments until the last segment when the number reaches its peak at 52. Type $A_2$ sensilla on the other hand increase from 37 on the first segment to the maximum of 68 on the second and 61 on the third segments. The number gradually decreases to its lowest of 16 on segment 13. C. pipiens and C. molestus follow the same general pattern.

The sensilla basiconica (A3) follow a pattern more similar to $A_1$ hairs than $A_2$. In C. fatigans, the minimum number of 12 is found on the first segment with the remaining 10 segments having a number between 14 and 23 (Fig. 10). The other two subspecies examined show similar patterns.

The only other kind of sensillum found is the sensilla companiformia (C). One or two were present on segment one, 10, 12 and 13. The numbers are constant in all three subspecies.

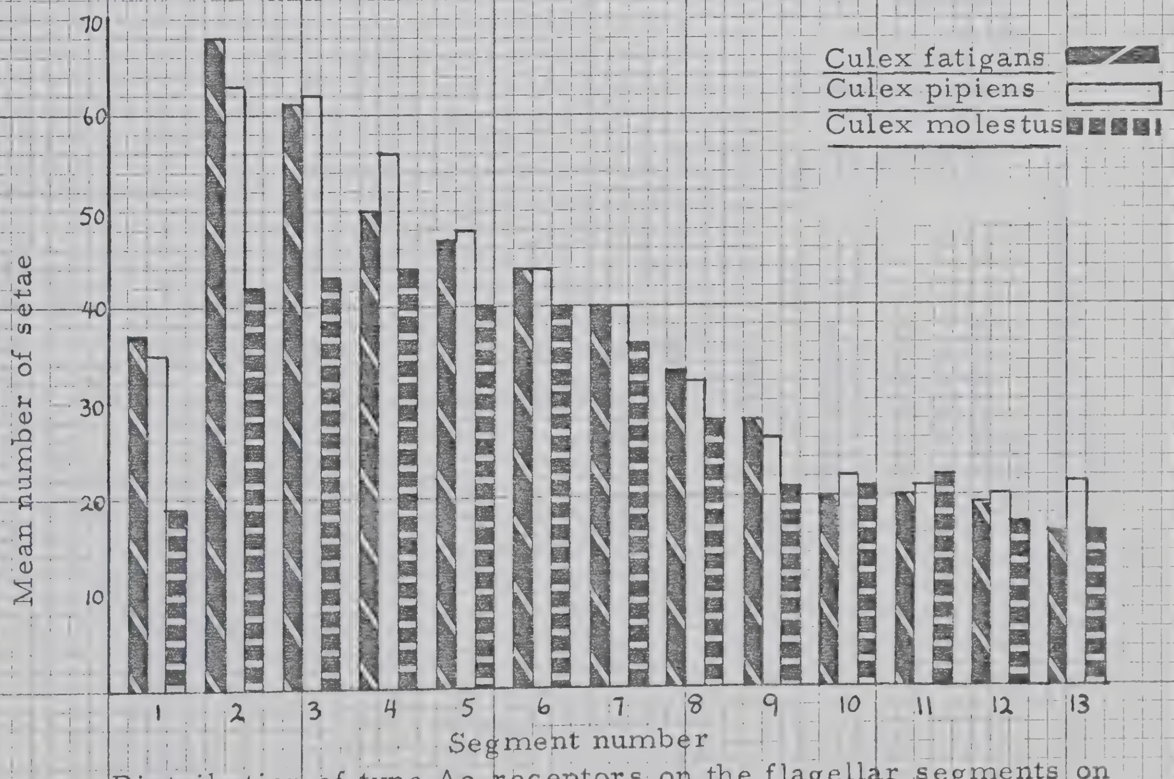
The three subspecies were compared for distribution differences of type $A_1$, $A_2$ and $A_3$ receptors. The following three histograms (Fig. 9 a, b & c) show that for the most part there is little difference in distribution pattern between the subspecies. The differences between distribution of each type of receptor for the entire flagellum of each subspecies could not be studied statistically using the student's t-test because of the significant differences in variance at the 1% level. When individual segments were compared the student's t-test could be applied. Only the segments which showed an obvious difference between subspecies

Fig. 9a



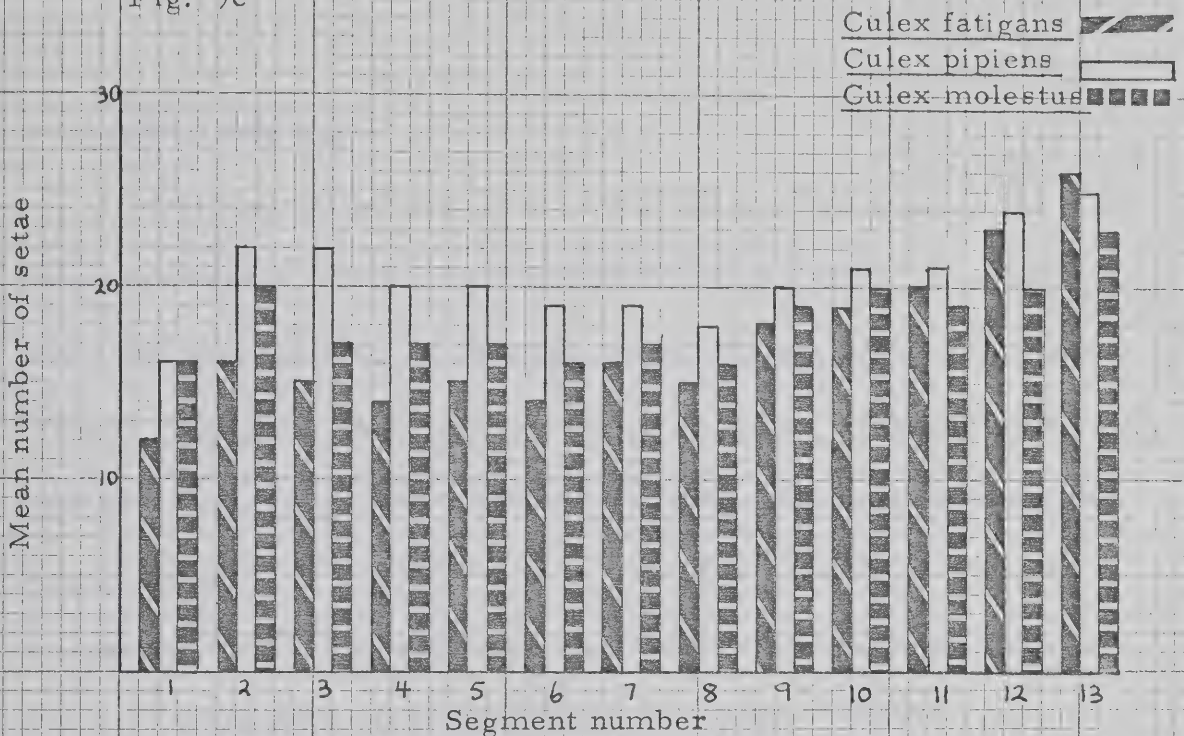

Distribution of type $A_1$ receptors on the flagellar segments on the antennae of female C. fatigans, C. pipiens and C. molestus.

Fig. 9b



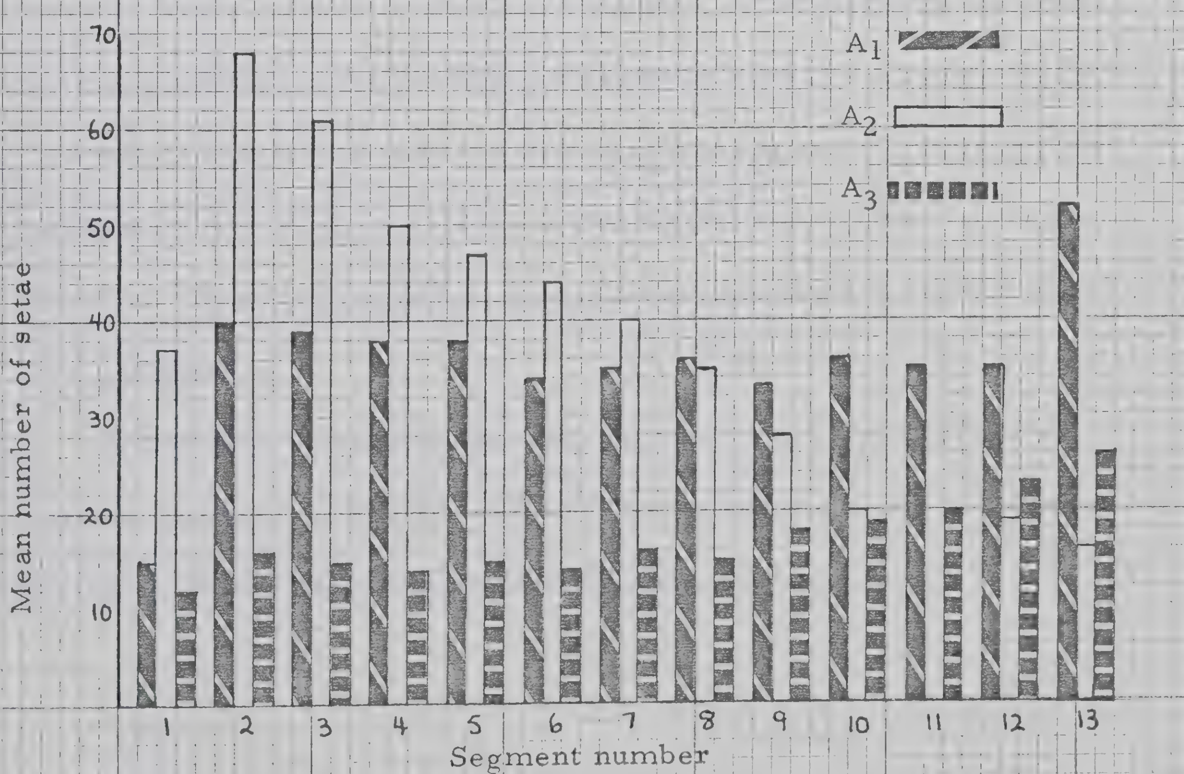

Distribution of type $A_2$ receptors on the flagellar segments on the antennae of female C. fatigans, C. pipiens and C. molestus.

Fig. 9c




Distribution of the $A_3$ receptors on the flagellar segments on the antennae of female C. fatigans, C. pipiens and C. molestus.

Fig. 10




Distribution of type $A_1$, $A_2$ and $A3$ receptors on the flagellar segments on the antennae of female C. fatigans.

were tested this way.

A significant difference at the 1% level is found between the three subspecies for type $A_1$ receptors on segment 13. Between segments one and four, C. fatigans and C. pipiens differ significantly from C. molestus in the number of $A_2$ receptors. Comparing type $A_3$ sensilla, C. fatigans was significantly different from C. pipiens and C. molestus from segments one to six. The difference between C. pipiens and C. molestus was significant over segments three to six. All differences were tested at the 1% level of significance.

The subspecies were also compared using the cumulative percentages of each type of receptor (Table II). The cumulative percentages of type $A_1$ sensilla over the flagellum differ little between the three subspecies. $A_2$ sensilla percentages reveal a closer resemblance between the distribution patterns of C. fatigans and C. pipiens than between these and C. molestus. The opposite is true for type $A_3$ sensilla. Here C. molestus most closely follows the percentages of C. pipiens.

The graphs of cumulative distribution (Figs. 11 and 12) show clearly what was said before about type $A_1$ and $A_3$ sensilla following the same general trend which differs from $A_2$ receptors.

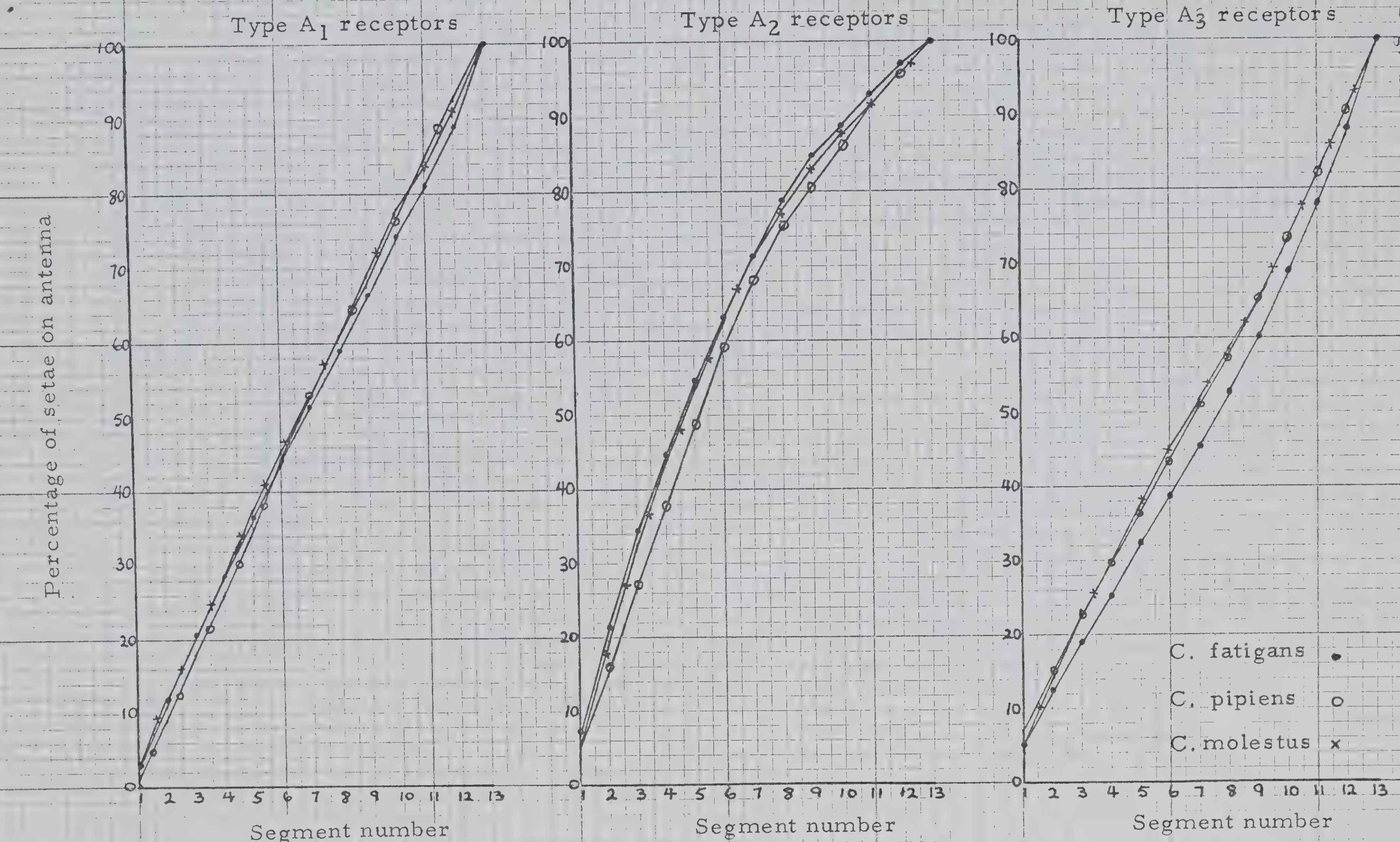
TABLE II

Cumulative percentages of the total of type $A_1$, $A_2$ and $A_3$ sensilla on the antennal flagellar segments of C.p. fatigans, C.p. pipiens and C.p. molestus females

| Flagellar Segment | $A_1$ | | | $A_2$ | | | $A_3$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | fatigans | pipiens | molestus | fatigans | pipiens | molestus | fatigans | pipiens | molestus |
| 1 | 3.3 | 1.5 | 2.6 | 7.5 | 5.0 | 7.1 | 5.3 | 6.6 | 5.8 |
| 2 | 11.9 | 9.3 | 11.2 | 21.6 | 15.8 | 19.8 | 12.5 | 15.0 | 14.2 |
| 3 | 20.4 | 18.1 | 20.8 | 34.3 | 26.8 | 32.4 | 19.2 | 22.2 | 22.3 |
| 4 | 28.5 | 26.1 | 28.5 | 44.7 | 37.9 | 43.7 | 25.6 | 29.5 | 29.9 |
| 5 | 36.6 | 35,3 | 37.0 | 54.3 | 48.3 | 53.6 | 32.2 | 36.5 | 37.3 |
| 6 | 44.1 | 44.2 | 45.0 | 63.3 | 58.7 | 62.4 | 38.7 | 43.5 | 44.8 |
| 7 | 51.5 | 52.6 | 52.9 | 71.6 | 67.9 | 70.6 | 45.8 | 50.6 | 51.8 |
| 8 | 59.2 | 60.5 | 60.3 | 78.8 | 75.1 | 77.5 | 52.4 | 57.4 | 58.4 |
| 9 | 66.4 | 67.7 | 68.9 | 84.7 | 80.5 | 82.8 | 60.3 | 65.2 | 65.8 |
| 10 | 74.2 | 76.2 | 76.8 | 88.8 | 82.8 | 87.5 | 69.0 | 73.6 | 73.8 |
| 11 | 81.3 | 84.5 | 83.9 | 93.0 | 91.5 | 91.7 | 78.0 | 81.6 | 81.9 |
| 12 | 88.9 | 92.6 | 91.0 | 97.0 | 95.8 | 95.8 | 88.4 | 90.2 | 90.9 |
| 13 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |

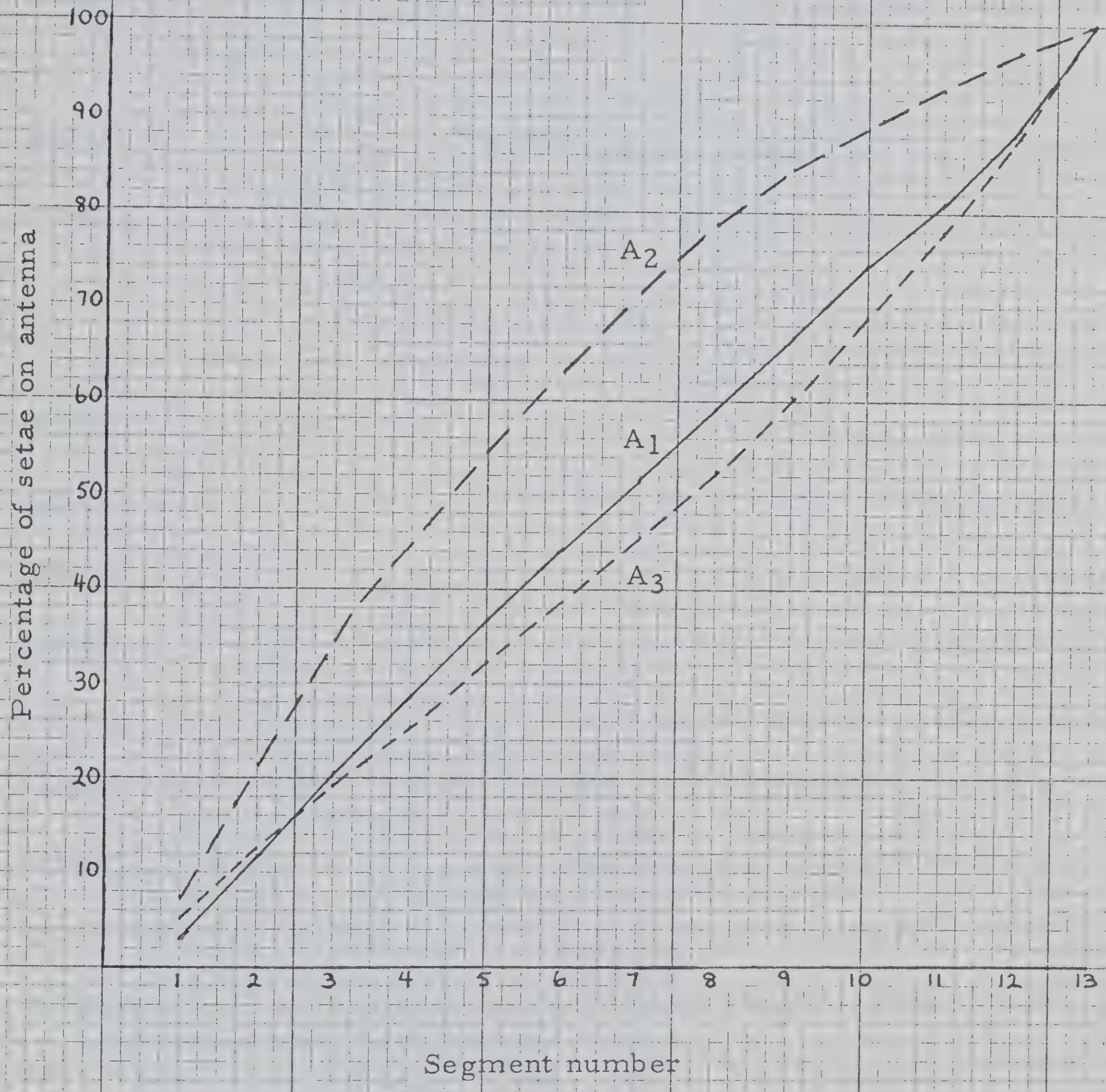
The values for C.p. fatigans are based on an average of 10 antennae; those of C.p. pipiens and C.p. molestus on 5 antennae. *all values are percentages.

Fig. 11




Cumulative distribution of setae on the antennal flagellum of C. fatigans, C. pipiens and C. molestus females.

Fig. 12




Cumulative distribution of setae on the antennal flagellum of C. fatigans females.

# 6. STRUCTURE OF OTHER RECEPTOR-BEARING ORGANS

While the antennae bear the greatest concentration of sensory receptors, it is of value to examine the other appendages for receptors which may be used in host-finding and feeding. In this study, the labrum, palps, labium, legs, wings, halteres and ovipositor of female C. fatigans were examined. All values given are the average of five mosquitoes examined.

## 6.1 The Labrum

Of the six stylets of the fascicle, the labrum is the stiffest and widest. It forms the dorsal surface of the food channel, lying mainly within the groove on the dorsal surface of the labium. I found the labrum of female C. p. fatigans had an average length of 1.8 mm and a width of 0.02 mm. It narrows to a point near the tip, resembling a pen tip. It is free of microtrichia and sensilla except for two groups near the tip. The proximal or subapical pair of sensilla, located about 0.18 mm from the tip in the ventrolateral edges of labrum, arise at the end of Vogel's chitin canals (1921), one on each side of the labrum. Each sensillum has a circular clear area about three microns in diameter surrounded by a dark rim. In the centre of the circle is a minute peg about 0.5 microns in diameter. von Gernet and Buerger (1966) thought these receptors resembled small basiconic sensilla surrounded by a membranous socket. Fig. 13 shows a faint clear spot at the lateral edge which is this sensillum. The peg within is not visible. The apical sensilla are located on the side of the

Fig. 13

0.1 mm


The tip of the labrum of C. fatigans in lateral view showing two sensilla. A apical sensillum. B subapical sensillum.

Fig. 14

0.5 mm


The labium and maxillary palps of C. fatigans.
Dorsal view.
La labellar lobes.
L labium.
M maxillary palp.

labral tip, each side having two very small bristles, one bristle being more distal and medial than the other. Because of their small size and location at the tip, further details could not be seen in my preparations. von Gernet and Buerger (1966) reported them to be hollow bristles set into membranous bases with fine dendrites innvervating them. Pearson (1970) concluded they were sensilla basiconica in A. aegypti. In Fig. 13, the base of the lateral one can be faintly seen.

6.2 The Labium (Fig. 14)

The labium of the female C.p. fatigans is about 2.1 mm long and has an average diameter of 0.06 mm. The greatest part of the labium is the elongated mentum lacking the palps. At the end of this are the labellar lobes (La) (about 0.19 mm long). Within the dorsal groove of the labium lie the stylets. The surface of the labium is striated, consisting of transverse bands of sclerotized and unsclerotized cuticle which give flexibility during the bending of the proboscis in feeding.

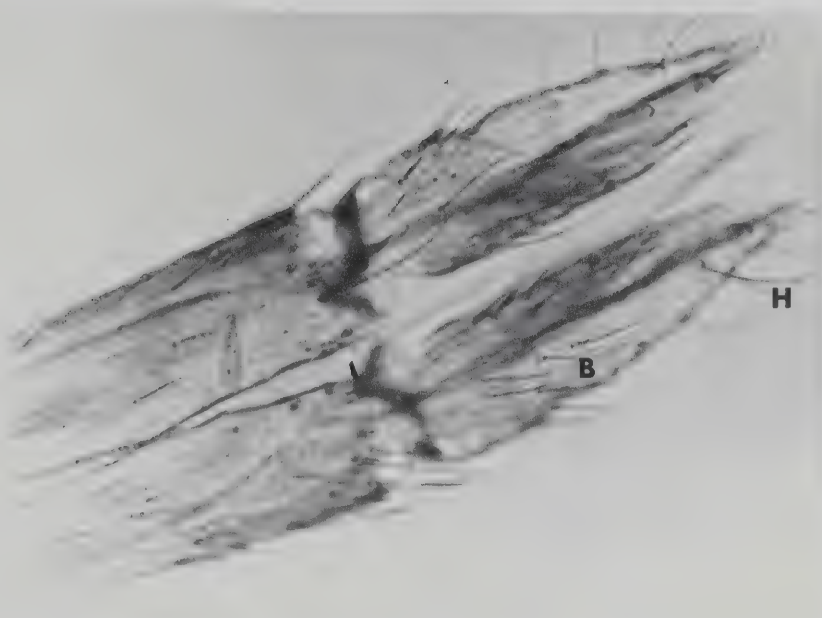
The base of the labium has a few large and small bristles on the ventral side. Microtrichia cover most of the surface. Scales are numerous except on the labellum and in the dorsal groove. Thick-walled, curved, pointed-tipped setae with sockets are found scattered amongst the scales. These bristles are about 65 microns long and 1.7 microns in diameter at their base. A ring of bristles is found on the mentum just proximal to the labella. Shorter (26.4 microns long) pointed-tipped

bristles with sockets are found scattered on the labium, mainly on the dorsal surface, but a few are located on the labellar tips and dorsal surface.

A labellar lobe of Culex fatigans consists of a basal medial part which is darkly sclerotized and a lighter lateral part extending to the tip. Thick-walled bristles about 46 microns long and curved at their tip, similar to those found on the remainder of the labium occur on the basal medial part (Fig. 15). Thick-walled hairs and small pegs as well as a few short bristles mentioned above are found on the lightly sclerotized dorso-lateral and ventro-lateral part of the lobes. The thick-walled hairs are pointed at the tip and about 53 microns long (Fig. 15). The base of the hair is set in a round, raised membrane surrounded by a sclerotized rim. The greatest number is on the ventro-lateral surface with some at the tips of the labella. These are similar to those reported on the labella of Culiseta inornata by Owen (1963) and on Aedes aegypti by Frings and Hamrum (1950) and Pearson (1970). Owen (1963) found that the hair terminated in a papilla. Similar hairs have been found on blowfly tarsi and labella and the electron microscope shows them to be double-lumened with an opening at the hair tip (Adams, Holbert and Forgash, 1965). Small thin-walled pegs about 6 microns long are distributed over the lightly pigmented part of the lobes, amongst the thick-walled hairs. These pegs are set in a large (3.5 micron diameter) membranous circular area. They are very thin-walled

Fig. 15

0.1 mm




The dorsal view of the tip of labium of C. fatigans showing the labellar lobes. H thick-walled hair, B bristles.

Fig. 16

0.05 mm


Third segment of the palp of C. fatigans. Ventral view. P thin-walled pegs.

and difficult to see with the light microscope. Their basal membranes are more visible than the pegs.

6.3 The Palps

The maxillary palps on the female mosquito consist of 4 segments; the terminal segment being small and set within the tip of the third segment. Only the extreme tip protrudes.

The first or basal segment is about 86 microns long and 55 microns wide. A major portion of the dorsal side lacks pigmentation. Four long bristles (0.13 mm to 0.26 mm) with sockets and three shorter, more slender bristles (0.055 mm to 0.060 mm) are located on the distal half of the surface. The entire surface is covered by microtrichia. There are several lateral scales.

The second segment averages 69 microns in length and 60 microns in width. Microtrichia occur over the whole surface. Located on the ventral surface are three long bristles and four or five shorter ones. There are many ventro-lateral scales. The dorsal surface, free of bristles and scales, is slightly concave and lighter in pigmentation. About three-quarters of the distance to the tip on the medial side is a single plate organ (sensillum placodeum), appearing as a slightly raised, circular clear membrance, surrounded by a heavier rim.

The third segment (Fig. 16) is 188 microns long and 56 microns in diameter at its widest part, tapering toward the distal end. The entire surface is covered with microtrichia. The dorso-lateral surface

has many scales which extend almost to the distal end. Amongst the scales are dispersed bristles 73 microns in length as well as a few pointed-tipped, thin-walled hairs 40 microns in length. These curve near their tips. The ventral surface has very few bristles and a few thin-walled hairs mainly located on the distal half of the segment. Most of the distal two-thirds of the ventral and medial surface is occupied by thin-walled pegs about 13 microns long whose base is set in a sunken membrane 4 microns in diameter.

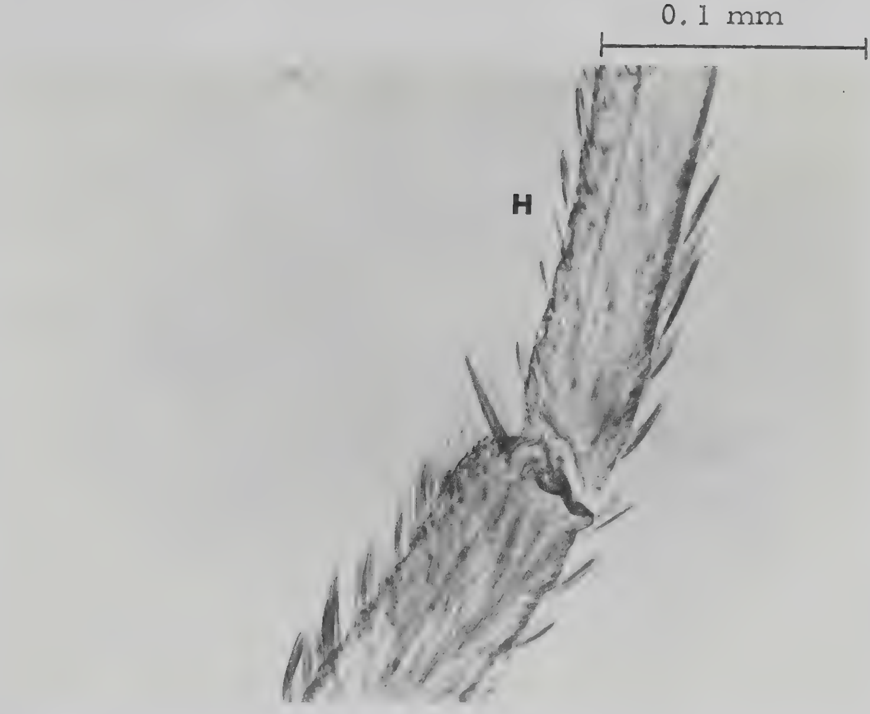
The fourth segment is very small and only the tip extends beyond the third segment. No sensilla other than microtrichia were seen on this segment.

6.4 The Legs

The parts of the female C. fatigans legs examined were the femur, tibia and five-segment tarsus. Since all the legs of C. fatigans bear similar receptors, the hind, middle and fore legs will be treated as one. The femur has a covering of microtrichia. Numerous scales cloak the surface except for a posterior part which touches the thorax. Two rows of large, heavy blunt-tipped bristles run the length of the femur. A cluster of medium, pointed-tipped bristles is found near the tip. A few small curved bristles 26 to 35 microns long are scattered mainly on the anterior surface of the femur.

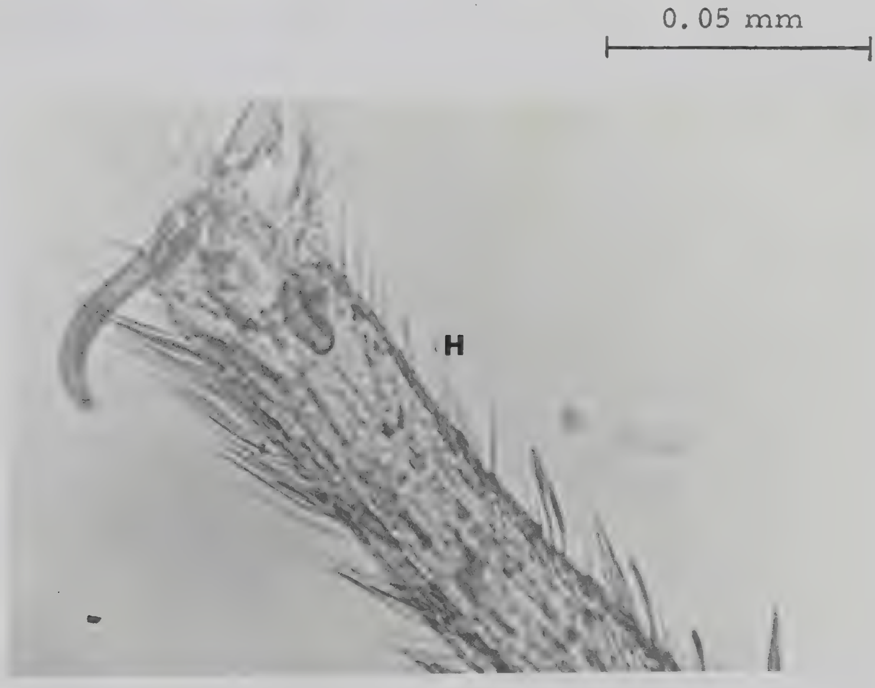
The tibia has a dense cover of scales and microtrichia. There are several rows of long, pointed-tipped and blunt-tipped, heavy bristles extending the length of the tibia. Two spine-like bristles

Fig. 17




Segment three and four of the tarsus of C. fatigans. Ventral view. H thick-walled hair.

Fig. 18




The tip of the fifth tarsal segment of the leg of C. fatigans. Ventral view. H thick-walled hair.

occur on the ventral side of the distal end. A cluster of medium-length bristles is located at the distal tip along with a few larger bristles. Small bristled (30 to 35 microns long) of the type found on the femur are sparsely scattered over the entire segment with a cluster at the end of the tibia. A few blunt-tipped thick-walled hairs with a double lumina are present on the ventral surface near the tip.

The five tarsal segments are similar. The distal tip of the fifth segment ends in two lateral claws (Fig. 18). All segments are densely covered by scales and microtrichia obscuring many of the smaller bristles and hairs. Several rows of pointed, long bristles and shorter, blunt bristles occur antero- and postero-ventrally on all segments but the fifth which bears only a few bristles at the tip. Two blunt, spine-like bristles are present ventrally at the distal tip of segments one, two, three and four (Fig. 17). A cluster of bristles of assorted sizes is found at the distal end of these segments. Small bristles of the type found on the rest of the leg are scattered over all tarsal segments. These bristles have thinner walls and are shorter and more slender than the other bristles found on the leg. They are found sparsely scattered on the femur, tibia and in increasing numbers on the tarsal segments. Blunt-tipped thick-walled hairs with a double lumina are located mostly on the ventral surface of the tarsus, increasing in density from segment one to five (Figs. 17 and 18). These hairs are about 27 microns long. Their base is set in a socket unlike those found on the labella. Dethier (1952, 1955) has proven electro-

physiologically that similar receptors on the blowfly are sensitive to sugar solutions as well as touch.

6.5 The Wings

The wings of the female Culex fatigans possess a covering of microtrichia with scales found along the veins. Pointed-tipped, small bristles are located on the anterior wing edge. Tactile hairs on the margins of Lepidoptera wings responding to air movements during flight have been reported by Vogel (1911).

6.6 The Halteres

These tiny bulb-like appendages, one on each side of the thorax below and behind the wing act as gyroscopes (Fraenkel and Pringle, 1938 and Pringle, 1948) which enable the insect to maintain its equilibrium during flight. Microtrichia cover the surface. Scales are located at the margin of the terminal bulb along with a few small bristles. The organs responsible for perceiving any stress in the cuticle of the base set up by rotation of the insect during flight are sensilla campaniformia arranged in two dorsal groups and one ventral group (called the "Hicks papilla") at the base of the halteres. According to Pringle, any movement of the insect out of the normal vertical plane of vibration of the halteres will cause lateral shearing forces in the cuticle of the haltere base causing the basal plate organs to respond. The other plates respond to the rate of oscillation of the haltere.

### 6.7 The Ovipositor

The valves of the ovipositor are covered with microtrichia. Small bristles and longer bristles are located along their margins. In these preparations no evidence was found for the presence of thin-walled receptors on the ovipositor. The small bristles present resemble those on the wing margin which may be mechanoreceptors.

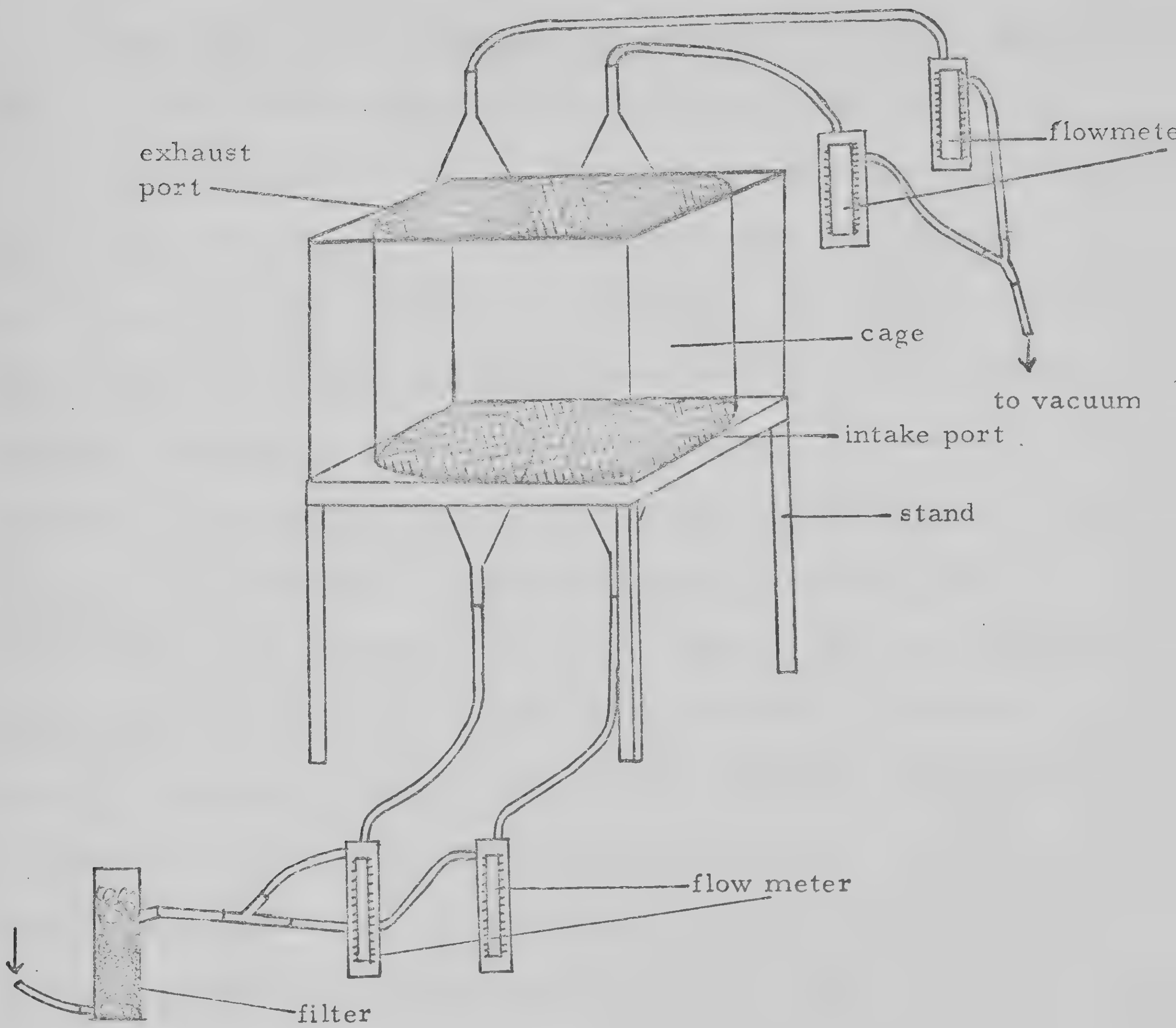
# 7. BEHAVIORAL WORK

## 7.1 Methods

An olfactometer is an apparatus designed to measure quantitatively the insect's response to odor. The insect is offered a choice of odor at two ports; the number of insects settled on each port is counted.

The olfactometer constructed for this experiment (see Fig. 19) was a modification of one type used by Steward (1959). It consisted of a plexiglas box 8" x 10" x 10" with two holes 4-1/2" in diameter on the top and two holes of the same diameter on the bottom. Over these holes were fitted four glass funnels - two serving as intake ports and two as exhaust ports. One end of the box opened to allow for insertion of an oval plexiglas cage covered with dacron mesh on top and bottom. This cage contained the mosquitoes and fitted snugly between the intake and exhaust ports. The end of the box was sealed with vaseline and held on tightly by elastic bands. The box was supported on a small wooden stand. An air filter of cotton and activated charcoal was inserted into the intake air line. Two flowmeters were connected before the intake ports and another two beyond the exhaust port. The exhaust lines were attached to a vacuum system. Two streams of air were therefore drawn upwards through the cage. The intake and exhaust rates could be regulated at each port so that the air streams were constant. There was little intermingling of the two streams as was evident when smoke was added to the intake air. One current was plain filtered air used as a control. The number of mosquitoes at each port was counted.

Fig. 19




A plexiglas olfactometer

7.2 Results

Twenty unfed female Culex fatigans were used in the preliminary test. They were placed in the olfactometer with an armpit sweat-soaked filter paper placed over one intake and plain filter paper placed over the other intake port. No preference to streams was recorded. The mosquitoes remained distributed at random on the top of the cage. When each of these filters was dipped in distilled water and reinserted into the air streams for a 10 minute interval, no preference was again recorded. Thompson and Brown (1955) reported that odor of perspiration is attractive to mosquitoes. Lipsitz and Brown (1964) found armpit sweat contained the attractive animo acids, arginine, threonine, tyrosine and lysine. My results did not substantiate this finding. Seventeen of these 20 mosquitoes landed and began to feed within five minutes after a washed and rinsed hand was placed on top of the cage. Because of the difficulty in finding an attractive substance which could be used in the olfactometer, further experimentation was abandoned.

## 8. DISCUSSION

Culex p. fatigans is a common vector for Wuchereria bancrofti in tropical countries. As such it is of medical importance. Control of the mosquito has proven difficult. It is therefore important to know as much about the morphology and physiology of this vector as possible.

Culex p. fatigans breeds in highly polluted water. Polluted water results in a significantly higher number of egg-rafts being deposited than non-polluted water. Ikeshoji (1966) exposed gravid C. fatigans to polluted and non-polluted water. He found that antennectomized females could not differentiate between the two waters while intact mosquitoes could. Steward and Atwood (1963) showed that antennectomized female Aedes aegypti would not respond to the human hand while those with the flagellum present alighted and probed.

The antennal flagellum of C. fatigans has three types of thin-walled receptors similar to those reported by Steward and Atwood (1963) and Slifer and Sekhon (1962) on the antenna of Aedes aegypti; by McIver (1969) on the antenna of Culex tarsalis and by Ismail (1964) on Culex fatigans and C. pipiens, Anopheles stephensi (Liston), A. gambiae (Giles) and A. maculipennis (Linnaeus). These sensory hairs are type $A_1$, $A_2$ type I and II and $A_3$. Type $A_1$ and $A_3$ receptors appear point-tipped under the light microscope, while $A_2$ hairs are definitely blunt-tipped. Recent work by Slifer (1970) revealed that when examined under higher power the pointed-tipped $A_1$ and $A_3$ hairs appear rounded. Therefore $A_1$, $A_2$ and $A_3$ receptors vary mainly in the length of the hair. These

receptors are all called sensilla basiconica by Schneider and Steinbrecht (1968). Snodgrass (1935) states "there is no sharply dividing line between sensilla trichodea and sensilla basiconica, either in the character of the external parts or in the structure of the internal parts".

Structurally, the thin-walled sensilla on C. fatigans resemble thin-walled pegs found on many other insect antennae (for a list see Slifer, 1967). I found crystal violet penetrated $A_1$ and $A_2$ hairs. As stated before, the dye only appeared in the distal half of the $A_1$ hair but in the entire $A_2$ hair. Slifer and Sekhon (1962) showed the cuticle of the $A_1$ hairs on the antennae of A. aegypti to be scalloped or grooved. Narrow openings pass through the sculptured wall. However, these authors were unable to find the relationship between the dendrites and the openings. Penetration of crystal violet into the lumen of intact $A_1$ hairs on C. fatigans indicates that openings do exist. The localization of the dye in the distal half of the hair lumen may indicate that the openings are present in the distal half of the hair wall. The intense and complete penetration of crystal violet into the $A_2$ hairs correlates well with the numerous pores (0.05 microns in diameter) found in the wall of the same receptor of A. aegypti by Slifer and Sekhon (1962). $A_3$ pegs did not stain. One explanation could be that given by McIver (1969). She found 50% of these pegs on C. tarsalis remained unstained. Because of their shortness, they may not come into contact with the dye which is applied by glass wool surrounding the antenna. Pores in the peg wall, which allow

the dye to penetrate to the lumen, are common among chemosensory hairs. They permit the stimulant to penetrate and make contact with the receptor dendrites. Contact receptors usually possess a single pore at the tip of the hair while olfactory receptors have many such pores. Two conflicting views of the relationship between pore opening and dendrite exist. Slifer and co-workers (1963, 1964a, b, c, 1970) found filaments, called "pore filaments", arising from the walls of the dendrites. Clusters of pore filaments extend into the pores where they are exposed to the air. Schneider (1969) gives the following account: "The pores may open into a pouch from which several tubules penetrate the inner parts of the cuticle and reach into the hair lumen nearly as far as the cell membrane of the dendrite. The tubules are not part of the dendrite or neurofilaments but are part of the cuticle. These tubules are present before the dendrite invades the lumen during morphogenesis. The innermost end of the tubule is clogged by material which looks different from that of the tubular wall. The canals lead the stimulant molecules into the fluid-filled lumen and eventually to the dendritic membrane". Ernst (1969) obtained conclusive evidence for this type of arrangement in the olfactory sensilla of Necrophorus.

Type $A_1$, $A_2$ and $A_3$ hairs of C. fatigans possess four to five neurones. Generally, most chemoreceptors have been found to have several neurones. The neurones occur in a group below each hair but because of the large number of hairs on the antennae of C. fatigans, they are often crowded together, making it difficult to discern the

number innervating any one hair. Because of the small size of the receptors, I found good sections, with cuticular and cellular components intact, were not easy to obtain. Finding a suitable stain posed another problem. Silver stains often gave capricious results but were used for detection of nerve tissue. Masson's trichrome and Heidenhain's iron haematoxylin stained most cells quite well. Even when these stains were used, the small size of these structures prevented me from observing cellular detail with the light microscope. Dendrites and axons were only occasionally seen.

Electron micrographs have contributed substantially to the present knowledge of the intricate inner detail of insect sensory receptors. Slifer (1970) gives a good review of the components of the chemoreceptive sensillum. The neurone cell body is narrow above the nucleus and here shows the structure of the cilium. Just below the cilium are one or two basal bodies. From the distal basal body, rootlets extend proximally. In cross-section, the basal bodies have nine sets of peripheral triplet tubules which become nine pairs of tubules distally. The ciliary region is only a few microns long. The dendrite is wider above the cilium and the tubules are continuous with the microtubules. Slifer and Sekhon (1969) proposed that the cilium and microtubules may be a cytoskeleton for the dendrites. Distal to the cilium, no cell organelles are found. The dendrites here consists of cell membrane, microtubules and probably fluid. Axons continue proximally into the antennal lumen where they join to form the antennal nerve that goes to the deutocerebrum. There

is no evidence of fusion of the axons. Moeck (1968) found in the ambrosia beetle, Trypodendron lineatum (Oliver) that the number of axons and neurones in the antenna were almost the same.

In my study the two associated epidermal cells, the trichogen and tormogen cells, were usually visible with the light microscope. They could be distinguished from the sensory neurones by having an irregularly shaped nucleus in which the chromatin was slightly more clumped than in the neurone nucleus. These two cells are responsible for the formation of the hair and basal membrane. They are often referred to as the sheath cells because they enclose the dendrites. In sections through the antennal flagellum of C. fatigans, I did not observe this wrapping around of the trichogen and tormogen cells. Slifer (1970) states: "the trichogen cell forms a closed ring that encircles the dendrites and its membranes from opposite sides meet in a well-defined junction". The tormogen cell is wrapped around the trichogen in the same way. There is a space between the trichogen and tormogen cells which is filled by fluid. In preserved material, this space appears as a vacuole. Slifer (1970) found microvilli on the cell walls exposed to the fluid. The fluid (or vacuole in fixed material) extends into the base of the hair. In my preparations, the vacuole appeared to be within the trichogen cell. However, the cell membrane of the trichogen cell could not be seen entirely and it is very likely that the vacuole is outside this cell. The dendrites are found within this space. In living cells, the fluid in the space is continuous with that in the hair lumen.

The bristles on the antennal flagellum of C. p. fatigans have the structure associated with mechanoreceptors. They have thick walls with no discernible openings in them. (Crystal violet did not penetrate intact bristles). They have sockets and only one sensory neurone whose dendrite ends at the bristle base.

The remaining type of sensillum on the antennae of C. p. fatigans is campaniform. These were first mentioned by Ismail (1962) in connection with the organs of the antennae of Anopheles maculipennis atroparvus and later (1964) found on C p. pipiens and C p. fatigans. Those found on segments one, 10 and 12 are similar in structure to sensilla campaniformia found on other parts of the body. It is generally agreed that they are mechanoreceptors responding to the bending of the cuticle. These, having a radially symmetrical dome without a longitudinal thickening, would react to bending in all directions. Their location at the distal end of the segment would enable them to detect cuticular stress when the flagellum is bent by air movement or in touching a surface. The two terminal campaniformia are difficult to classify. They are different from the other campaniformia. It is unlikely that they function as pressure sensitive receptors since they are located within pits. Electron micrographs and electrophysiological recordings are necessary to determine their structure and function, and as yet neither has been made.

The antennal flagellum of C. fatigans bears a total of approximately 1300 receptors of which about 1200 are thin-walled receptors

which probably are chemosensory. It was thought that by comparing the distribution of antennal receptors on C. pipiens subspecies with different feeding patterns some clue to receptor function could be obtained. This proved fruitless since the distribution patterns of $A_1$, $A_2$ and $A_3$ receptors are not significantly different statistically for the three subspecies, C. fatigans, C. pipiens and C. molestus.

In 1964, Ismail published a paper comparing the distribution of receptors on female culicini and anophelini mosquitoes. His work includes counts on C. fatigans and C. pipiens. Table 10 in the Appendix gives Ismail's results. The results of his counts and mine (compare with Table I) are nearly the same. Some differences do appear. For type $A_1$ and $A_2$, his values for C. pipiens are lower than mine and for C. fatigans slightly higher. The number of $A_3$ receptors is similar to my counts. The differences which do occur can be accounted for in part, by the difficulty in finding all the receptors when the number is large and in part by the differences which may be present in various strains of the same subspecies. It is likely that the strains Ismail used at the Swiss Tropical Institute were not those used by myself.

The pattern of distribution of receptors is needed if one is to do behavioral studies such as were initially planned in this work. Upon studying the cumulative percentages of type $A_1$, $A_2$ and $A_3$ receptors on the flagellum, it is evident that successive amputation of segments would yield doubtful results. The first seven segments have half the total number of type $A_1$ and $A_3$ receptors. Half the total number of

type $A_2$ receptors are located on the first five segments. Even with only two segments remaining on the flagellum, 12 to 22% of all $A_1$, $A_2$ and $A_3$ receptors still remain. When an olfactometer was set up and initial attempts to elicit a response using armpit sweat as an attractant failed, this method of determining the function of a receptor was questioned. Behavioral studies in the past have been inconclusive. The over-lapping distribution of types of sensilla on an antennal segment does not allow a definite function to be given to a certain receptor type on the basis of the insect's behavior after obliteration of the segment. Steward and Atwood (1963) concluded on the basis of behavioral work, that receptors of type $A_1$ and perhaps $A_3$ on the antennae of _A. aegypti_ were concerned with attractancy and type $A_2$ receptors with repellancy. $A_3$ sensilla were thought to be thermoreceptors rather than chemoreceptors. Roth and Willis (1952) believed $A_2$ receptors were hygroreceptors. Slifer and Brescia (1960) decided the $A_2$ sensilla may act as hygroreceptors, or as general chemical receptors, or as olfactory receptors, on the basis of their structure in _A. aegypti._

Recent electrophysiological studies by Lacher (1967) ascertained the function of $A_1$, $A_2$ and $A_3$ receptors as olfactory. $A_1$ neurones are inhibited by essential oils and excited by fatty acids. $A_2$ receptor cells are inhibited by $C_{2-5}$ fatty acids and excited by $C_{7-10}$ fatty acids. Type $A_3$ cells are excited by fatty acids. Kellogg (1970) reported type $A_3$ sensilla to respond to water vapor. This receptor was capable of

detecting a sudden increase of 2% in relative humidity. The type $A_3$ sensillum may be a case where only one neurone responds to the water vapor while another or other neurones respond to odor.

Sensory receptors occur on other parts of the mosquito as well as on the antennae. In this study, only the external parts of these receptors were examined.

The two types of receptors found on the labrum are apparently chemosensory in function. von Gernet and Buerger (1966) suggest that the labral receptors may be used in detecting food, making the preliminary distinction between blood and sugar. However, Pearson (1970) could not detect any electrical response from the apical sensilla to various chemical or mechanical stimuli and concluded they were vestigial receptors. The labellar contact chemoreceptors are well known. Such receptors are also present on the tarsal segments. Adams, Holbert and Forgash (1965) did an electron microscopic investigation of these receptors on the labella and tarsi of Stomoxys calcitrans (Linnaeus). They found the distal tip of the hair has a pore open to the exterior. One dendrite ends at the base of the hair. The remaining four enter the thick-walled lumen where they extend to the open tip. Slifer (1962) found these hairs with permeable tips on the tarsi of A. aegypti. Hodgson and Roeder (1956) determined electrophysiologically that one neurone of the blowfly receptor mediated sugar reception and another salt, while Mellon and Evans (1961) detected a third neurone responding to water. A fourth neurone is sensitive to mechanical stimulation (Wolbarsht and Dethier, 1958).

Pearson (1970) only elicited a response to mechanical deflection from these labellar hairs of Aedes aegypti. Ikeshoji (1966) extirpated the mouth parts and legs of C. fatigans and tested their response to breeding waters. He found the tarsal contact receptors detect deterrents such as salt in the water, while ovipositional arrestants such as protein, were detected by the proboscis, especially the labium. In this regard, the work done by Owen (1963) on the contact chemoreceptors of Culiseta inornata is relevant. Water and sugar applied to the chemosensory hairs on the labella evoked a feeding response while blood did not. Owen (1963) suggested the receptors located within the cibarium control sucking. The stimuli which attract the mosquito to the host also elicit the sucking response.

As far as is known, no work has been done on the thin-walled pegs I found on the labella of C. fatigans. It would be interesting to find out what part they play in the feeding response. The same holds true for the single sensillum placodeum found on the second segment of the maxillary palps. The palps bear many peg receptors which Kellogg (1970) found by electrophysiological methods to respond to carbon dioxide. He determined that one neurone was sensitive to sudden increases in carbon dioxide concentration from 0.01% to the saturation level of 0.05% to 0.5%. Other neurones in the same receptor responded independently to other vapors. Willis and Roth (1952) found A. aegypti females to be attracted to carbon dioxide. Roth (1951) concluded that the palpi receive olfactory stimuli when the mosquito lands on or is near the host's skin. He thought

the palpi possess temperature receptors. As well as the pegs, thin-walled hairs occur on the third segment of the palpi and these may be thermoreceptors. Proof of their function requires further work.

## 9. CONCLUSIONS

The sense organs on the antennae of Culex fatigans were studied with the light microscope. Six types of sensilla are found on both male and female antennae. The number and distribution of these receptors differ greatly in the two sexes.

Two types of sensilla chaetica are present. The first type are large bristles found mostly in whorls and are more numerous and longer on the male than female antennae. The second type are smaller bristles not arranged in whorls but usually present at the distal end of each flagellar segment. There is an overlap of length between the two types. Structurally both types appear to be mechanoreceptors.

Three types of thin-walled sensilla are found on all flagellar segments of the female but only on the two distal segments of the male. These three types of sensilla are:- pointed-tipped ($A_1$) and blunt-tipped ($A_2$) sensilla trichodea and thorn-shaped sensilla basiconica ($A_3$). Each receptor has at least four sensory neurones as well as a trichogen and a tormogen cell. Basal bodies associated with the cilium are found in the dendrites of $A_3$ pegs. Type $A_1$ and $A_2$ hairs are permeable to crystal violet dye indicating the presence of pores in the hair wall. Type $A_3$ pegs did not stain but this may be due to their short length rather than lack of pores in the peg wall. Types $A_1$, $A_2$ and $A_3$ receptors all have the appearance of chemoreceptors.

Sensilla campaniformia are located on the first, 10th, 12th and tip of the 13th segments of female C. fatigans. The sensilla on the

first, 10th and 12th segment are alike in structure and different from the two in the cones at the tip of segment 13. Except for the terminal campaniformia it is probable that the sensilla campaniformia function as pressure or stress receptors.

The pedicel of both male and female C. fatigans is almost entirely occupied by a complex scolopophorous Johnston's organ. It is well documented as an organ of hearing as well as detection of flagellar movement.

The distribution of the sensilla on the antennae of female C. fatigans, C. pipiens and C. molestus were compared. In each subspecies, the distribution pattern of type $A_1$ hairs resembles that of type $A_3$ pegs more closely than that of type $A_2$ hairs. Type $A_2$ hairs decreased in number toward the flagellar tip while type $A_1$ hairs and $A_3$ pegs remained fairly constant in number with a slight increase towards the flagellar tip. The distribution of each receptor type proved significantly different statistically on only a few segments when all three subspecies were compared.

Female C. fatigans has thick-walled hairs on its tarsi and labella which are probably contact chemoreceptors. Sensilla basiconica which function as chemoreceptors are present on the palps. The base of the halteres bear several fields of sensilla campaniformia, acting as receptors of cuticular stress or distortion. Bristles similar to those on the antennae are located on the labium, palps, legs, ovipositor, halteres and wings. These bristles are probably mechanoreceptors.

An olfactometer was built to study the effect of successive amputation of flagellar segments on the behavioral response of C. fatigans females to odor. Armpit sweat, concentrated or diluted, did not elicit any response when twenty unfed females were tested.

## 10. LITERATURE CITED

Adams, J.R., Holbert, P.E. and A.J. Forgash. 1965. Electron Microscopy of the contact chemoreceptors of the stable fly, Stomoxys calcitrans (Diptera; Muscidae). Ann. ent. Soc. Am. 58 : 909-917.

Bar-Zeev, M. 1960. The location of hygroreceptors and moisture receptors in Aedes aegypti L. Ent. exptl. Appl. 3 : 251-256.

Clements, A.N. 1956. The antennal pulsating organs of mosquitoes and other Diptera. Quart. J. Microscop. Sci. 97 : 429-433.

Child, C.M. 1894. Ein bisher wenig beachtites antennales Sinnesorgan der Culiciden und Chironomeden. Zeit. wiss. Zool. 58 : 475-528.

Dethier, V.G. 1952. Adaptation to chemical stimulation of tarsal receptors of the blowfly. Biol. Bull. Wood's Hole. 103 : 178-189.

Dethier, V.G. 1953. Chemoreception, in Insect Physiology; 544-576. Roeder, K.D., Ed., John Wiley and Sons, Inc., New York.

Dethier, V.G. 1954. The physiology of olfaction in insects. Ann. N.Y. Acad. Sci. 58 : 139-157.

Dethier, V.G. 1955. The physiology and histology of the contact chemoreceptors of the blowfly. Quart. Rev. Biol. 30 : 348-371.

Dethier, V.G. and L.E. Chadwick. 1948. Chemoreception in insects. Physiol. Rev. 28 : 220-254.

Dethier, V.G. and M.L. Wolbarsht. 1956. The electron microscopy of chemosensory hairs in Phormia regina Meig. Experientia 12 : 335-337.

Dostal, B. 1958. Riechfahigkeit und Zahl der Riechsinneselemente bei der Honigbiene. A. vergleich. Physiol. 41 : 179-203.

Eggers, F. 1924. Zur Kenntnis der antennalen Stiftfuhrenden Sinnesorgane der Insekten. Zeit. Morph. Oekol. Tiere 2 : 259-349.

Ernst, K.D. 1969. Die Feinstruktur von Riechsensillen auf der Antenne des Aaskafers Necrophorus (Coleoptera). Z. Zellforsch, mikroskop. Anat. 94 : 72-102.

Feir, D., Lengy, J.I. and W.B. Owen. 1961. Contact chemoreception in the mosquito, Culiseta inornata Williston; sensitivity of the tarsi and labella to sucrose and glucose. J. Insect Physiol. 6 : 13-20.

Forel, A. 1908. The sense of insects. Methuen and Co. Ltd. London.

Fraenkel, G. and J.W.S. Pringle. 1938. Halteres of flies as gyroscopic organs of equilibrium. Nature Lond. 141 : 919-920.

Frings, H. and M. Frings. 1949. The loci of contact chemoreceptors in insects. Am. Midl. Nat. 41 : 602-658.

Frings, H. and C.L. Hamrum. 1950. The contact chemoreceptors of the adult yellow fever mosquito, Aedes aegypti. J.N.Y. ent. Soc. 58 : 133-142.

Hodgson, E.S. 1955. Problems in invertebrate chemoreceptors. Quart. Rev. Biol. 30 : 331-347.

Hodgson, E.S. 1958. Chemoreception in arthropods. Ann. Rev. Ent. 3 : 19-36.

Hodgson, E.S. and K.D. Roeder. 1954. Electrical response of insect chemosensory neurons to normal stimuli. Anat. Rec. 120 : 718.

Hodgson, E.S. and K.D. Roeder. 1956. Electrophysiological studies of arthropod chemoreception. J. cell. comp. Physiol. 48 : 51-75.

Hsu, F. 1938. Étude cytologique et comparée sur les sensilles des Insectes. La Cellule 47 : 1-60.

Ikeshoji, T. 1966. Studies on mosquito attractants and stimulants. Part. I. Chemical factors determining the choice of oviposition sites by Culex pipiens fatigans and pallens. Jap. J. Exp. Med. 36 : 49-59.

Ikeshoji, T. 1966. Studies on mosquito attractants and stimulants. Part III. The presence in mosquito breeding waters of a factor which stimulates oviposition. Jap. J. Exp. Med. 36 : 67-72.

Ismail, I.A.H. 1962. Sense organs in the antennae of Anopheles maculipennis atroparvus v. Thiel and their possible function in relation to the attraction of female mosquito to man. Acta Trop. 19 : 1-58.

Ismail, I.A.H. 1964. Comparative study of sensory organs in the antennae of Culicine and Anopheles female mosquitoes. Acta Trop. 21 : 155-168.

Johnston, C. 1855. Auditory apparatus of Culex mosquito. Quart. J. Microscopy 3 : 97-102.

Kellogg, F.E. 1970. Water vapor and carbon dioxide receptors in Aedes aegypti L. J. Insect Physiol. 16 : 99-108.

Lacher, V. 1967. Electrophysiologische Untersuchungen an einzelnen Geruchsrezeptoren auf den Antennen weiblicher Moskitos (Aedes aegypti L.) J. Insect Physiol. 13 : 1461-1471.

Larsen, J. R. 1960. The use of Holme's silver stain on insect nerve tissue. Stain Technology 35 : 223-224

Larsen, J.R. 1962. The fine structure of the labellar chemosensory hairs of the blowfly, Phormia regina Meig. J. Insect Physiol. 8 : 683-691.

Lehmann, M. C. G. 1799. De antennis Insectorium, 2 Pt., Londoni.

Lipsitz, E.Y. and A.W.A. Brown. 1964. Studies on the response of the female Aedes mosquito. IX. The mode of attractiveness of lysine and other amino acid. Bull. ent. Res. 54 : 675-687.

Marshall, J. 1935. The location of olfactory receptors in insects. A review of experimental evidence. Trans. R. ent. Soc.. Lond. 83 : 49-72.

Mayer, A.M. 1874. Experiments on the supposed auditory apparatus of the mosquito. Am. Nat. 8 : 577-592.

McIver, S. 1969. Antennal sense organs of female Culex tarsalis (Diptera Culicidae). Ann. ent. Soc. Am. 62 : 1455-1461.

Mellon, D. and D.R. Evans. 1961. Electrophysiological evidence that water stimulates a fourth sensory cell in the blowfly taste receptor. Am. Zool. 1 : 372.

Minnich, D.E. 1929. The chemical senses of insects. Quart. Rev. Biol. 4 : 100-112.

Moeck, H.A. 1968. Electron microscopic studies of antennal sensilla in the ambrosia beetle Trypodendron lineatum (Oliver) (Scolytidae). Can. J. Zool. 46 : 521-556.

Morita, H. 1959. Initiation of spike potentials in contact chemosensory hairs of insects. III. D.C. stimulation and generator potential of labellar chemoreceptor of Calliphora. J. cell. comp. Physiol. 54 : 189-204.

Morita, H. and K. Takeda. 1959. Initiation of spike potentials in contact chemosensory hairs in insects. II. The effect of electric current on tarsal chemosensory hairs of Vanessa. J. cell. comp. Physiol. 54 : 177-187.

Owen, W.B. 1963. The contact chemoreceptor organs of the mosquito and their function in feeding behavior. J. Ins. Physiol. 9 : 73-87.

Palade, G.E. 1952. A study of fixation for electron microscopy. J. exp. Med. 95 : 285-297.

Pearson, T.R. 1970. The structure and function of the apical labral pegs and long labellar hairs of the mosquito Aedes aegypti (L.). Ph. D. thesis, University of Alberta, Edmonton, Alberta

Pringle, J.W.S. 1948. The gyroscopic mechanism of the halteres of Diptera. Phil. Trans. Roy. Soc. B. 233: 347-384.

Pumphrey, R.J. and E. G. Gray. 1958. Ultrastructure of the insect ear. Nature Lond. 181 :618.

Risler, H. 1953. Das Gehörorgan der Männchen von Anopheles stephensi Liston (Culicidae). Zool. Jahrb. 73 : 165-186.

Risler, H. 1955. Das Gehororgan der Mannchen von Culex pipiens L., Aedes aegypti L. and Anopheles stephensi Liston (Culicidae), eine vergleichend morphologische Untersuchung. Zool. Jahrb. 74 : 478-490.

Roth, L.M. 1948. A study of mosquito behavior. An experimental laboratory study of the sexual behaviour of Aedes aegypti (Linn). Am. Midl. Nat. 40 : 265-352.

Roth, L.M. 1951. Loci of sensory end-organs used by mosquitoes Aedes aegypti (L.) and Anopheles quadrimaculatus (Say) in receiving host stimuli. Ann. ent. Soc. Am. 44 : 59-74.

Roth, L.M. and E.R. Willis. 1952. Possible hygroreceptors in Aedes aegypti (L.) and Blattella germanica (L.) J. Morph. 91 : 1-14.

Schneider, D. 1957. Electrophysiological investigations on the antennal receptors of the silk moth during chemical and mechanical stimulation. Experientia 13 : 89-91.

Schneider, D. 1964. Insect antennae. Ann. Rev. Ent. 9 :103-122.

Schneider, D. 1969. Insect olfaction: Deciphering systems for chemical messages. Science (Washington) 163 : 1031-1037.

Schneider, D. and K.E. Kaissling. 1957. Der Bau der Antenne des Seidenspinners Bombyx mori L. II Sensillen, cuticulare Bildungen und innerer Bau. Zool. Jahrb. (Anat. Ontog. Tiere) 76 : 223-250.

Schneider, D. and R.A. Steinbrecht. 1968. Checklist of insect olfactory sensilla, in Invertebrate Receptors : 279-297. Carthy, J.D. and G. E. Newell, Eds. Academic Press Inc. London and New York.

Slifer, E. H. 1960. A rapid and sensitive method for identifying permeable areas in the body wall of insects. Ent. News 71 : 179-182.

Slifer, E.H. 1962. Sensory hairs with permeable tips on the tarsi of the yellow-fever mosquito, Aedes aegypti. Ann. ent. Soc. Am. 55 : 531-535.

Slifer, E.H. 1967. The thin-walled olfactory sense organs on insect antennae, in Insects and Physiology : 233-245. Beament, J.W.L. and J.E. Treherne, Eds. Oliver and Boyd, Edinburgh.

Slifer, E.H. 1970. Anthropod chemoreceptor structure. Ann. Rev. Ent. 15 : 121-142.

Slifer, E.H. and V.T. Brescia. 1960. Permeable sense organs on the antenna of the yellow fever mosquito, Aedes aegypti (Linnaeus). Ent. News 71 : 221-225.

Slifer, E.H., Prestage, J.J. and H.W. Beams. 1959. The chemoreceptors and other sense organs on the antennal flagellum of the grasshopper (Orthoptera: Acrididae). J. Morph. 105 : 145-191.

Slifer, E.H. and S.S. Sekhon. 1961. Fine structure of the sense organs on the antennal flagellum of the honey bee, Apis mellifera Linnaeus. J. Morph. 109 : 351-381.

Slifer, E.H. and S.S. Sekhon. 1962. The fine structure of the sense organs on the antennal flagellum of the yellow fever mosquito, Aedes aegypti (Linnaeus). J. Morph. 111 : 49-67.

Slifer, E.H. and S.S. Sekhon. 1963. Sense organs on the antenna of the small milkweed bug, Lygaeus kalmii Stal (Hemiptera, Lygaeidae). J. Morph. 112 : 165 - 193.

Slifer, E.H. and S.S. Sekhon. 1964a. Fine structure of the sense organs on the antennal flagellum of a flesh fly, Sarcophaga argyrostoma R.-D. (Diptera, Sarcophagidae). J. Morph. 114 : 185-207.

Slifer, E.H. and S.S. Sekhon. 1964b. Fine structure of the thin-walled sensory pegs on the antenna of a beetle, Popilius disjunctus (Coleoptera, Passalidae). Ann. ent. Soc. Am. 57 : 541-548.

Slifer, E.H. and S.S. Sekhon. 1964c. The dendrites of the thin-walled olfactory pegs of the grasshopper (Orthoptera, Acrididae). J. Morph. 114 : 393-410.

Slifer, E.H. and S.S. Sekhon. 1969. Some evidence for the continuity of ciliary fibrils and microtubules in the insect sensory dendrite. J. Cell. Sci. 4 : 527-540.

Snodgrass, R.E. 1926. The morphology of insect sense organs and the sensory nervous system. Smithsonian Misc. Coll. 77(8) : 80 pp.

Snodgrass, R.E. 1935. Principles of Insect Morphology. McGraw-Hill Book Co., Inc. New York and London : 667 pp.

Spielman, A. 1964. Population structure in the Culex pipiens complex of mosquitoes. Bull. Wld. Hlth. Org. Geneva, 31 Aug.-4 Sept. 1964.

Steward, C.C. 1959. The sense organs of mosquitoes. Ph. D. dissertation, Univ. of Toronto, Ont.

Steward, C.C. and C.E. Atwood. 1963. The sensory organs of the mosquito antenna. Can. J. Zool.41 : 577-594.

Tateda, H. and H. Morita. 1959. Initiation of spike potential in contact chemosensory hairs of insects. I. Generating site of the recorded spike potentials. J. cell. comp. Physiol. 54 : 171-176.

Thompson, R.P. and A.W.A. Brown. 1955. The attractiveness of human sweat to mosquitoes and the role of carbon dioxide. Mosq. News 15 :80-84.

Vogel, R. 1911. Uber die Innervierung der Schmetterlings - Flugel and Uber den Bau and die Verbreitung der Sinnes-organe auf denselben. Z. wiss. Zool. 98 : 68-134.

Vogel, R. 1921. Zur Kenntnis der Geruchsorgane der Wespen und Bienen. Zool. Anz. 53 : 20-28.

von Frisch, K. 1921. Uber den Sitz des Geruchssinnes bei Insekten. Zool. Jahrb. 38 : 449-516.

von Frisch, K. 1935. Uber den Geschmackssinn der Bienne. Zeit. vergl. Physiol. 21 : 1-156.

von Gernet, G. and G. Buerger. 1966. Labral and cibarial sense organs of some mosquitoes. Quaest. Ent. 2 : 259-270.

Willis, E.R. and L.M. Roth. 1952. Reaction of Aedes aegypti (L.) to carbon dioxide. J. exp. Zool. 121 : 149-179.

Wolbarsht, M. L. 1958. Electrical activity in the chemoreceptors of blowfly. II. Responses to electrical stimulation. J. gen. Physiol. 42 : 413-428.

Wolbarsht, M. L. and V. G. Dethier. 1958. Electrical activity in the chemoreceptors of the blowfly. I. Responses to chemical and mechanical stimulation. J. gen. Physiol. 42: 393-412.

Table 1

Distribution of type $A_1$ receptors on the antennae of female C.p. fatigans

| Specimen | Segment Number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1 | 18 | 36 | 39 | 37 | 38 | 31 | 33 | 35 | 30 | 36 | 28 | 30 | 51 |
| 2 | 17 | 36 | 39 | 38 | 39 | 32 | 34 | 34 | 33 | 36 | 33 | 35 | 50 |
| 3 | 13 | 42 | 38 | 39 | 38 | 37 | 34 | 38 | 34 | 37 | 30 | 32 | 51 |
| 4 | 15 | 43 | 39 | 37 | 37 | 36 | 36 | 39 | 35 | 37 | 31 | 37 | 53 |
| 5 | 17 | 43 | 39 | 39 | 38 | 35 | 34 | 39 | 32 | 37 | 33 | 34 | 51 |
| 6 | 13 | 40 | 38 | 37 | 36 | 34 | 32 | 34 | 33 | 33 | 34 | 36 | 50 |
| 7 | 14 | 40 | 39 | 38 | 36 | 34 | 37 | 38 | 34 | 35 | 35 | 36 | 56 |
| 8 | 15 | 42 | 39 | 37 | 38 | 35 | 36 | 32 | 34 | 37 | 34 | 37 | 53 |
| 9 | 16 | 41 | 43 | 40 | 42 | 37 | 38 | 35 | 34 | 38 | 35 | 36 | 54 |
| 10 | 14 | 40 | 38 | 37 | 36 | 34 | 36 | 36 | 35 | 36 | 34 | 36 | 51 |
| Mean | 15.2 | 40.3 | 39.1 | 37.9 | 37.8 | 34.5 | 35.0 | 36.0 | 33.4 | 36.2 | 32.7 | 34.9 | 52.0 |
| Standard Deviation | 1.75 | 2.58 | 1.45 | 1.10 | 1.81 | 1.96 | 1.89 | 2.40 | 1.51 | 1.40 | 2.31 | 2.28 | 1.94 |

Table 2

Distribution of type $A_2$ receptors on the antennae of female C.p. fatigans

| Specimen | Segment Number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1 | 41 | 68 | 60 | 46 | 46 | 40 | 40 | 38 | 28 | 20 | 20 | 18 | 14 |
| 2 | 40 | 69 | 61 | 50 | 49 | 45 | 40 | 36 | 32 | 19 | 19 | 19 | 15 |
| 3 | 33 | 69 | 63 | 46 | 47 | 45 | 41 | 31 | 29 | 19 | 18 | 18 | 15 |
| 4 | 36 | 68 | 59 | 47 | 46 | 45 | 40 | 36 | 27 | 20 | 21 | 19 | 16 |
| 5 | 36 | 67 | 63 | 51 | 46 | 46 | 41 | 36 | 28 | 20 | 21 | 19 | 16 |
| 6 | 34 | 66 | 58 | 51 | 50 | 40 | 37 | 32 | 27 | 20 | 21 | 18 | 16 |
| 7 | 36 | 69 | 64 | 55 | 46 | 46 | 41 | 36 | 32 | 24 | 21 | 19 | 16 |
| 8 | 35 | 68 | 61 | 50 | 46 | 44 | 41 | 36 | 26 | 20 | 19 | 17 | 16 |
| 9 | 38 | 71 | 63 | 54 | 46 | 42 | 41 | 32 | 26 | 20 | 19 | 19 | 16 |
| 10 | 36 | 68 | 61 | 53 | 44 | 42 | 40 | 36 | 30 | 20 | 20 | 19 | 17 |
| Mean | 36.5 | 68.3 | 61.3 | 50.3 | 46.6 | 43.5 | 40.2 | 34.9 | 28.5 | 20.2 | 19.9 | 18.5 | 15.7 |
| Standard Deviation | 2.51 | 1.34 | 1.95 | 3.20 | 1.71 | 2.32 | 1.23 | 2.33 | 2.22 | 1.40 | 1.10 | 0.71 | 0.82 |

Table 3

Distribution of type $A_3$ receptors on the antennae of female C. p. fatigans

| Specimen | Segment Number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1 | 14 | 16 | 14 | 15 | 15 | 15 | 15 | 15 | 18 | 19 | 20 | 26 | 26 |
| 2 | 13 | 15 | 15 | 15 | 15 | 16 | 16 | 15 | 19 | 20 | 20 | 24 | 26 |
| 3 | 12 | 16 | 14 | 15 | 16 | 15 | 18 | 14 | 20 | 22 | 21 | 24 | 27 |
| 4 | 12 | 16 | 17 | 15 | 16 | 15 | 17 | 15 | 20 | 21 | 21 | 24 | 26 |
| 5 | 11 | 15 | 17 | 15 | 17 | 16 | 17 | 15 | 19 | 21 | 20 | 24 | 26 |
| 6 | 11 | 15 | 14 | 12 | 14 | 14 | 16 | 14 | 15 | 18 | 21 | 23 | 25 |
| 7 | 12 | 17 | 14 | 13 | 12 | 12 | 14 | 14 | 15 | 17 | 19 | 20 | 25 |
| 8 | 11 | 17 | 14 | 14 | 14 | 13 | 15 | 14 | 16 | 18 | 18 | 23 | 26 |
| 9 | 11 | 18 | 17 | 13 | 15 | 14 | 16 | 14 | 17 | 18 | 21 | 20 | 25 |
| 10 | 11 | 15 | 12 | 14 | 13 | 14 | 15 | 15 | 17 | 18 | 20 | 22 | 26 |
| Mean | 11.8 | 16.0 | 14.8 | 14.1 | 14.7 | 14.4 | 15.9 | 14.5 | 17.6 | 19.2 | 20.1 | 23.0 | 25.8 |
| Standard Deviation | 1.03 | 1.05 | 1.69 | 1.10 | 1.49 | 1.26 | 1.20 | 0.53 | 1.90 | 1.69 | 0.98 | 1.89 | 0.63 |

Table 4

Distribution of $A_1$ receptors on the antennae of female C.p. molestus

| Specimen | Segment Number 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 5 | 37 | 38 | 34 | 42 | 40 | 37 | 33 | 32 | 38 | 36 | 37 | 30 |
| 2 | 9 | 32 | 38 | 31 | 39 | 36 | 35 | 34 | 29 | 37 | 34 | 32 | 33 |
| 3 | 7 | 33 | 37 | 35 | 37 | 38 | 38 | 34 | 32 | 36 | 37 | 35 | 30 |
| 4 | 5 | 31 | 36 | 33 | 39 | 36 | 33 | 34 | 31 | 34 | 33 | 36 | 30 |
| 5 | 5 | 33 | 39 | 37 | 38 | 39 | 32 | 32 | 30 | 36 | 36 | 34 | 32 |
| Mean | 6.2 | 33.2 | 37.6 | 34.0 | 39.0 | 37.8 | 33.4 | 33.4 | 30.8 | 36.2 | 35.2 | 34.8 | 31.0 |
| Standard Deviation | 1.79 | 2.28 | 1.14 | 2.24 | 1.86 | 1.79 | 0.89 | 0.89 | 1.28 | 1.48 | 1.63 | 1.91 | 1.41 |

Table 5

Distribution of $A_2$ receptors on the antennae of female C.p. molestus

| Specimen | Segment Number 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 20 | 42 | 44 | 45 | 42 | 42 | 38 | 30 | 24 | 23 | 23 | 18 | 15 |
| 2 | 20 | 43 | 42 | 44 | 40 | 43 | 35 | 28 | 19 | 21 | 20 | 15 | 20 |
| 3 | 20 | 43 | 44 | 42 | 42 | 38 | 35 | 29 | 20 | 21 | 23 | 16 | 17 |
| 4 | 18 | 43 | 42 | 44 | 37 | 40 | 33 | 28 | 19 | 20 | 20 | 18 | 15 |
| 5 | 19 | 40 | 42 | 43 | 41 | 39 | 39 | 27 | 23 | 19 | 23 | 18 | 15 |
| Mean | 19.4 | 42.2 | 42.8 | 43.6 | 40.4 | 40.4 | 36.0 | 28.4 | 21.0 | 20.8 | 21.8 | 17.0 | 16.4 |
| Standard Deviation | 0.89 | 1.30 | 1.11 | 1.14 | 2.01 | 2.08 | 2.45 | 1.14 | 2.35 | 2.10 | 1.64 | 1.41 | 2.19 |

Table 6

Distribution of type $A_3$ receptors on the antennae of female <u>C. p. molestus</u>

| Specimen | Segment Number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1 | 17 | 22 | 20 | 20 | 18 | 18 | 18 | 17 | 22 | 22 | 20 | 20 | 25 |
| 2 | 18 | 22 | 18 | 17 | 16 | 18 | 16 | 16 | 19 | 20 | 18 | 20 | 23 |
| 3 | 14 | 19 | 14 | 15 | 16 | 17 | 18 | 16 | 20 | 20 | 18 | 20 | 25 |
| 4 | 15 | 18 | 16 | 17 | 19 | 14 | 16 | 16 | 16 | 17 | 21 | 21 | 22 |
| 5 | 15 | 19 | 18 | 17 | 15 | 16 | 17 | 16 | 16 | 21 | 19 | 21 | 21 |
| Mean | 15.8 | 20.0 | 17.2 | 17.2 | 16.8 | 16.6 | 17.0 | 16.2 | 18.6 | 20.0 | 19.2 | 20.4 | 23.2 |
| Standard Deviation | 1.64 | 1.82 | 2.28 | 1.79 | 1.64 | 1.67 | 1.00 | 0.45 | 2.61 | 1.86 | 1.30 | 0.55 | 1.79 |

Table 7

Distribution of type $A_1$ receptors on the antennae of female <u>C. p. pipiens</u>

| Specimen | Segment Number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1 | 11 | 38 | 42 | 39 | 40 | 36 | 34 | 32 | 38 | 36 | 35 | 32 | 39 |
| 2 | 11 | 39 | 42 | 38 | 37 | 36 | 36 | 32 | 35 | 36 | 35 | 34 | 41 |
| 3 | 14 | 43 | 45 | 40 | 41 | 39 | 39 | 40 | 41 | 37 | 33 | 31 | 41 |
| 4 | 13 | 39 | 41 | 40 | 41 | 37 | 36 | 40 | 38 | 38 | 35 | 35 | 43 |
| 5 | 13 | 41 | 41 | 40 | 40 | 40 | 41 | 40 | 40 | 35 | 34 | 32 | 47 |
| Mean | 12.4 | 40.0 | 42.2 | 39.4 | 39.8 | 37.6 | 37.2 | 36.8 | 38.4 | 36.4 | 34.4 | 32.8 | 42.2 |
| Standard Deviation | 1.34 | 2.00 | 1.64 | 0.89 | 1.64 | 1.82 | 2.77 | 4.38 | 2.30 | 1.14 | 0.89 | 1.64 | 3.03 |

Table 8

Distribution of type $A_2$ receptors on the antennae of female <u>C. p. pipiens</u>

| Specimen | Segment Number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1 | 34 | 63 | 61 | 56 | 47 | 42 | 40 | 31 | 27 | 20 | 18 | 20 | 21 |
| 2 | 33 | 62 | 61 | 55 | 48 | 43 | 39 | 34 | 27 | 21 | 20 | 19 | 20 |
| 3 | 36 | 63 | 64 | 55 | 52 | 45 | 41 | 36 | 29 | 25 | 24 | 19 | 21 |
| 4 | 35 | 64 | 63 | 56 | 49 | 43 | 40 | 34 | 27 | 24 | 24 | 20 | 21 |
| 5 | 35 | 61 | 59 | 56 | 45 | 45 | 40 | 34 | 22 | 21 | 19 | 24 | 21 |
| Mean | 34.6 | 62.6 | 61.6 | 55.6 | 48.2 | 43.6 | 40.0 | 33.8 | 26.4 | 22.2 | 21.0 | 20.4 | 20.8 |
| Standard Deviation | 1.14 | 1.12 | 1.95 | 0.55 | 2.59 | 1.34 | 0.71 | 1.79 | 2.61 | 2.17 | 2.83 | 2.07 | 0.45 |

Table 9

Distribution of type $A_3$ receptors on the antennae of female <u>C. p. pipiens</u>

| Specimen | Segment Number | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| 1 | 13 | 20 | 20 | 19 | 16 | 17 | 16 | 16 | 15 | 18 | 21 | 20 | 22 |
| 2 | 14 | 21 | 19 | 18 | 19 | 17 | 17 | 16 | 16 | 18 | 20 | 22 | 22 |
| 3 | 17 | 26 | 23 | 21 | 21 | 22 | 19 | 19 | 22 | 23 | 22 | 25 | 27 |
| 4 | 17 | 23 | 24 | 20 | 22 | 21 | 20 | 19 | 22 | 23 | 20 | 26 | 26 |
| 5 | 17 | 20 | 22 | 22 | 21 | 21 | 21 | 18 | 23 | 24 | 23 | 26 | 26 |
| Mean | 15.6 | 22.0 | 21.6 | 20.0 | 19.8 | 19.6 | 18.6 | 17.6 | 19.6 | 21.2 | 21.3 | 23.8 | 24.6 |
| Standard Deviation | 1.95 | 2.55 | 2.07 | 1.58 | 2.39 | 2.41 | 2.07 | 2.30 | 3.78 | 2.95 | 1.30 | 2.68 | 2.41 |

Table 10

Distribution and number of long and short bristles and sensilla trichodea, basiconica and campaniformia on the antennae of <u>C. fatigans</u> and <u>C. pipiens</u> by I. A. H. Ismail (1964)*

| | Type I Long Bristles | | Type II Short Bristles | | Type III Sensilla Trichodea | | | | Type IV Sensilla Basiconica | | Type VI Sensilla Campaniformia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | with pointed tip | | with blunt tip | | | | | |
| Flagellar Segment | C. fatigans | C. pipiens | C. fatigans | C. pipiens | C. fatigans | C. pipiens | C. fatigans | C. pipiens | C. fatigans | C. pipiens | C. fatigans | C. pipiens |
| 1 | Undifferentiated | | | | 14 | 5 | 34 | 25 | 11 | 13 | 2 | 2 |
| 2 | 6 | 6 | 8 | 8 | 40 | 29 | 69 | 62 | 14 | 22 | 0 | 0 |
| 3 | 6 | 6 | 6 | 6 | 39 | 32 | 63 | 61 | 17 | 21 | 0 | 0 |
| 4 | 6 | 6 | 3 | 5 | 39 | 36 | 56 | 54 | 14 | 20 | 0 | 0 |
| 5 | 6 | 6 | 2 | 4 | 38 | 38 | 50 | 51 | 17 | 19 | 0 | 0 |
| 6 | 6 | 6 | 1 | 3 | 36 | 35 | 47 | 46 | 16 | 18 | 0 | 0 |
| 7 | 6 | 6 | 2 | 2 | 37 | 35 | 41 | 39 | 16 | 20 | 0 | 0 |
| 8 | 6 | 6 | 1 | 2 | 39 | 34 | 36 | 35 | 15 | 19 | 0 | 0 |
| 9 | 6 | 6 | 1 | 1 | 35 | 33 | 28 | 28 | 20 | 18 | 0 | 0 |
| 10 | 6 | 6 | 1 | 1 | 37 | 33 | 20 | 23 | 22 | 22 | 1 | 1 |
| 11 | 6 | 6 | 1 | 1 | 35 | 33 | 21 | 19 | 21 | 21 | 0 | 0 |
| 12 | 6 | 6 | 1 | 1 | 37 | 36 | 19 | 17 | 24 | 25 | 1 | 1 |
| 13 | 6+4 | 6+4 | 0 | 0 | 53 | 45 | 16 | 17 | 26 | 27 | 2 | 2 |
| Total | 76 | 76 | 27 | 34 | 479 | 424 | 500 | 477 | 233 | 265 | 6 | 6 |

The figures given are the average of five independent counts. *This table included for comparison with my data.